

**2004-2005 Final Report:
A pilot study and assessment of the efficacy of invertebrates as
indicators of meadow change in Sierra Nevada Network Parks**



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Summary

The Sierra Nevada Network initiated an agreement with the University of California White Mountain Research Station to assess invertebrates as indicators of meadow change. Additional baseline ecological data on the meadow invertebrate assemblage was needed prior to testing response of projected invertebrate vital signs to meadow change. Particular needs included information on fine-scale temporal changes through the growing season, more intensive aquatic phase sampling, comparative sampling in both subalpine and montane meadows, and assessment of relationships between invertebrates, vegetation, and physical parameters. A pre-project report/literature review was also requested and has been delivered.

We sampled meadow habitat intensively through the 2004 and 2005 growing seasons, including both aquatic and emergent portions of meadows. Sites were located in the subalpine Tuolumne Meadows system of Yosemite National Park and a series of montane meadows near the Giant Forest in Sequoia National Park. In Tuolumne, we sampled a series of sites weekly through the dynamic first three to four months of the season and then continued bi-weekly sampling until road closure. At the Giant Forest, we sampled bi-weekly during the first two months of the season followed by monthly sampling until snowfall. We sampled aquatic habitat with a throw trap and terrestrial habitat with a

vacuum net. We also performed efficiency tests on the sampling apparatus and tested catch characteristics of vacuum nets, pitfall traps, and sweep nets.

Predictor variables sampled included: gram dry mass of both standing crop and litter, litter depth, water or air temperature, relative humidity, canopy height, soil penetration pressure, soil moisture, gross percent cover estimates, vegetation dominants, water depth, water flow, percent cover by plant species, overall patch size, and water table depth. Primary faunal response variables included: overall abundances and abundances by order and family, as well as abundances as a factor of standing crop and canopy height, biomass, species richness, and Margalef's species richness.

Throw trapping and vacuum netting both produced quantitative density data. Pitfall trapping did not sample flying fauna and provided only catch-per-unit-effort data. Conversely, sweep nets captured flying fauna well, but collected proportionally fewer beetles and ants relative to vacuum netting. Although sweep nets are also only catch-per-unit-effort tools, these devices have appeal for monitoring, because the nets are easy to use, light, fast, produce samples that require minimal sorting, avoid wilderness restrictions, integrate a larger sampling area, and yield reproducible data with variances that are no higher than produced by vacuum netting.

We collected eighteen families of aquatic fauna in Tuolumne over two years and 27 families in the Giant Forest in a single year. Family richness of terrestrial fauna was greater in the Giant Forest as well; the 91 families collected in Sequoia National Park represented almost twice the family richness found in Tuolumne. Dominant aquatic taxa included mosquitos, mayflies, and stoneflies, whereas mites, ants, and ground beetles were the dominant terrestrial fauna. Large numbers of aquatic snails and bivalves were also collected in the montane meadows. Aquatic assemblage structure was similar in Tuolumne in the longer, dryer 2004 growing season and the shorter, wetter 2005 with the same taxa dominating, and terrestrial family richness was almost identical during the two years. Abundances were also stable across the two years, and this consistency suggests that this system will produce good signal-to-noise ratios in a long term monitoring plan.

Abundance was generally high across all habitats, and we sorted and identified about 61,000 individuals: 45,000 individuals in the main study, plus 8,000 in sweep nets and a similar number in the pitfall study. That said, distinct trends emerged. In the subalpine meadows, abundances of fauna were much greater in flooded habitat (present only during the first month or two after melt-off) than in dry portions of meadows. These early season “rivers of grass” present in the first month after snowmelt appeared to be strikingly important to

the meadow-dominated ecosystem. In the montane meadows, terrestrial fauna were much more abundant than aquatic fauna, probably due to a longer growing season, higher soil moisture, and tall canopy.

Early season was the most important for overall faunal production. Most aquatic habitat disappears after the first two months of the season, and these ponded areas are very productive. Further, terrestrial arthropods increased throughout the early part of the summer, reached a peak in the second or third month after snowmelt and then decreased throughout the remainder of the season. This pattern was remarkably consistent for most terrestrial taxa. Land managers generally try to ease pressure on meadows during the early, wet portion of the growing season, and this practice benefits fauna as well.

Carex utriculata harbored high abundances of fauna in both flooded and dry habitat. *C. utriculata* was a dominant where this plant occurred in our subalpine meadows and made up the majority of sampled aquatic vegetation but represented a relatively small amount of total terrestrial habitat. *Antennaria* sp. rarely dominated but harbored high numbers of terrestrial fauna. Canopy height was the coarse predictor with the most overall influence, particularly for the terrestrial fauna.

We advocate monitoring invertebrates at the assemblage/family-level, making use of both aquatic and terrestrial taxa, complemented by genus and/or

species level analyses of ants. The broad family level surveys would provide extensive taxonomic monitoring, whereas monitoring ant populations would provide a good fine-scale response. We recommend use of three catch-per-unit-effort tools: sweep nets for terrestrial faunal surveys, D-frame nets for aquatic sampling, and baiting for sampling ants. We believe that these first two years of study, and associated literature review, should provide assurance that invertebrates can be efficiently sampled, that taxonomy can be manageable, and that there is sufficient signal-to-noise ratio to reliably detect spatial and temporal trends.

Introduction

National Park Service (NPS) policy and recent legislation (National Parks Omnibus Management Act of 1998) requires that park managers know the condition of natural resources under NPS stewardship and monitor long-term trends in those resources in order to fulfill the NPS mission of conserving parks unimpaired. The NPS has developed an Inventory & Monitoring program to fill knowledge gaps in baseline data on natural resources in parks and to design and implement long-term (Vital Signs) monitoring that will enable managers to develop broadly-based, scientifically sound information on the current status and long term trends in the composition, structure, and function of park ecosystems (Fancy 2003).

The Sierra Nevada Network initiated an agreement with White Mountain Research Station to assess invertebrates as indicators of meadow change. Meadows are of high interest for monitoring as these habitats concentrate resources, provide critical habitat for both resident and transient animals, and have been identified as key ecosystem elements in the Sierra Nevada Network Parks. A powerful indicator of the status of meadow ecosystems is found in the invertebrate assemblages that use meadows for all or part of their life cycles. Meadow invertebrates are ideal candidates for monitoring, because these animals 1) include representatives of several trophic levels and are important

food resources and processors of organic material, 2) represent a “crossroads” for ecological flows, e.g., aquatic-terrestrial, 3) are easy to sample quantitatively, and 4) are sensitive to a variety of stresses and in turn are capable "vectors" for cascading disturbances (Holloway 1980, Rosenberg et al. 1986). In particular, invertebrates are sensitive to trampling pressures (e.g., Liddle 1975, Hylgaard 1980) and arthropod populations can be reduced by nearby trails in the Sierra (Holmquist & Schmidt-Gengenbach 2004). Invertebrates are also extremely sensitive to pesticides, herbicides and other contaminants (Curry 1994, Cilgi & Jepson 1995, Scholtz & Krüger 1995, Longley & Sotherton 1997, Ellsbury et al. 1998, Stewart 1998).

Additional baseline ecological data on the meadow invertebrate assemblage were needed in order to establish potential metrics for use as vital signs. Particular needs included information on fine-scale temporal changes of the invertebrate assemblage through the growing season, more information on aquatic phase fauna, assessment of relationships between invertebrates and vegetation, determining differences in assemblage structure between subalpine and montane meadows, and documenting correlations between a broad suite of physical parameters and fauna. The ecological information gleaned from this initial pilot work will provide necessary background for selecting parameters that will ensure efficiency of vital sign usage (Andersen & Majer 2004). This work

will also identify potential cost savings via timing of sampling, sampling and sample sorting methodologies, taxonomic resolution, and choice of efficient response variables.

A pre-project report/literature review was also requested and has been delivered (Holmquist 2004). This report explores the importance of invertebrates in ecosystem function, role of invertebrates in trophic webs, invertebrates as links among habitats, response of invertebrates to disturbance, ecology and natural history of alpine meadow invertebrates, history and potential of invertebrates as vital signs, and available sampling methodologies.

Methods

We sampled meadows intensively through the 2004 and 2005 growing seasons, including both aquatic and emergent habitat (Figs. 1, 2). All Yosemite sites were in the large, non-wilderness Tuolumne Meadows system (Figs. 3, 4), and Sequoia sites were located in Crescent, Log, and Huckleberry Meadows, near the Giant Forest (Fig. 5). Tuolumne Meadows is a subalpine system at 2604-2619m and, whereas the Giant Forest meadows are montane and lie at 2043-2062m. We sampled a series of sites from initial melt-off until snowfall in Tuolumne in 2004 and 2005 and in the Giant Forest in 2005 only. Tuolumne sampling ran from 13 May through 16 October in 2004 and from 10 June through 26 October following the heavier snowfall of 2005. We sampled in the Giant Forest from 19 May through 24 October 2005.

Aquatic samples in Tuolumne were taken weekly until standing water was no longer present in the meadows after one to two months (Tables 1, 2). We collected one to three samples per week for a total of twelve aquatic samples in 2004 and fourteen in 2005. We collected three aquatic samples bi-weekly in the Giant Forest over the first two months after melt-off (twelve samples total; Table 3).

Terrestrial samples in Tuolumne were taken weekly (typically three samples per week) through the dynamic first three to four months of the

season followed by three samples bi-weekly until road closure (48 and 46 samples total in 2004 and 2005, respectively; Tables 1, 2). In the Giant Forest, we collected six terrestrial samples bi-weekly during the first two months after melt-off, followed by six samples per month until snowfall (48 total samples; Table 3). All aquatic and terrestrial samples were collected from randomly-chosen locations within suitable habitat (Figs. 3-5).

Aquatic fauna. We sampled aquatic habitat with a throw trap (Fig. 6) which is a quantitative device for sampling still, shallow water with submerged and/or emergent vegetation (Kushlan 1981, Holmquist et al., 1989). The throw trap (or drop trap) is a box lacking a solid top or bottom that is cleared of fauna with a net. The trap has been shown to be highly efficient, relative to other collecting devices, for quantitatively sampling fauna in vegetated aquatic habitats (Kushlan 1981, Jacobsen & Kushlan 1987, Rozas & Minello 1997). Throw trapping of well-separated stations is effectively sampling with replacement (Jacobsen & Kushlan 1987), and re-sampling vegetated sites at four to six month intervals over a period of four years does not cause shifts in measures of vegetation cover or assemblages of mobile fauna (Holmquist et al. 1989; J.G. Holmquist, pers. obs.). Throw traps have been used in a number of habitats including freshwater marshes (Erwin et al. 1985, Jordan et al. 1994, Ruetz et al. 2005), shallow seagrass beds (Holmquist et al. 1989), seagrass

several meters below the surface (Holmquist 1997), and flooded Mojave playas (Brostoff et al. submitted), and have recently been used in a Devils Postpile National Monument inventory (Holmquist and Schmidt-Gengenbach 2005).

We used a device and protocol derived from that of Kushlan (1981) and Holmquist et al. (1989). The trap was a 0.75 m x 0.75 m box without a top or bottom and constructed of sheet aluminum. The clearing device was a 0.75 m-wide framed and handled net (bar seine) with 0.5 mm square mesh. The trap was thrown downwind (Fig. 6) and then pressed into the sediment. The bar seine was passed repeatedly through the trap (Fig. 7) for a minimum of ten passes and until three successive passes produced no additional animals. The bar seine was washed in a tub until free of fauna after each pass (Fig. 7). We then immediately sorted fauna (live) from vegetation. Samples with particularly large numbers of animals were subsampled with a plankton splitter (Fig. 8)

Terrestrial fauna. We sampled terrestrial habitat with a vacuum net apparatus (Fig. 9). Vacuums with nets inserted in the intake tube generally offer an improvement in efficiency over other methods of sampling invertebrates in vegetation, and this technique has been used in a variety of studies (e.g., Richmond and Graham 1969, Hand 1986, Macleod et al. 1994), including at least one Park Service monitoring program (Fellers and Drost 1991). Vacuums are more efficient than visual censuses (Arnold et al. 1973) or sweep netting

(e.g., Dietrick et al. 1960, Arnold et al. 1973, Buffington and Redak 1998), especially for ground dwellers (New 1998), because sweep netting underestimates ground-dwelling invertebrates (Whittaker 1952, Hughes 1955). This increased efficiency incorporates both abundance and species richness (Buffington and Redak 1998). Vacuums also cause less damage to invertebrates than sweep netting (Callahan et al. 1966) and are particularly efficient at removing animals in litter and lower vegetation (Stewart and Wright 1995). Vacuum sampling has been found to be most efficient when used with some form of enclosure box which is placed prior to suctioning (Henderson and Whittaker 1977, Hower and Ferguson 1972, Harper and Guynn 1998), although enclosures are often not used.

Despite the general efficiency of vacuum sampling, this method has not worked well in capturing rapidly-moving insects (Powell et al. 1996). The operator creates disturbance, and even if an enclosure box is used, flying and other vagile insects will flee the area before the enclosure is placed. Much of the efficiency of throw trapping is a function of the “throwing,” i.e., by tossing the trap from a distance, animals are captured before the field personnel are detected by the fauna. In an effort to create a terrestrial analog to the throw trap, Holmquist and Schmidt-Gengenbach (2002), constructed a 0.5 m² steel quadrat with a conical mesh covering (Fig. 9). The mesh cone has an elasticized

hole at the apex through which a vacuum intake tube can be inserted. This quadrat is thrown toward the target area from a distance and staked in place to form a seal with the substrate. The vacuum intake is then inserted through the mesh aperture for sampling (Fig. 9).

We used a Craftsman 320 km/h gasoline vacuum modified with a nylon “no-see-um” mesh (0.25mm) collecting chamber inserted in the intake tube in conjunction with the netted quadrat (Fig. 9). Henderson and Whittaker (1977) and Hossain et al. (1999) found that vacuum sampling is most efficient if initial vacuum passes are made and then followed by clipping of vegetation and additional vacuuming. After staking the quadrat, we made multiple passes through the vegetation with the vacuum intake from different orientations over a two-minute period. Then the intake was removed, and the vegetation was clipped with trimmers inserted through the elasticized aperture of the netted quadrat. The trimmers were then removed and the intake inserted for an additional two minutes of sampling. The intake was then extracted from the quadrat, the integral mesh collecting bag was removed from the intake tube, and the fauna and litter were transferred to a re-sealable plastic bag and placed on ice. Sorting was done at the laboratory.

Aquatic and terrestrial taxa were identified to family. During pre-project NPS-UC WMRS meetings, we decided that taxonomy at the family level would be

a good starting point for this pilot study and would provide a good cost-benefit ratio. Further, there has been good success in using family-level identifications in monitoring programs (e.g. Hilsenhoff 1988)

Vacuum net efficiency. As we sought a method as efficient across a wide range of fauna as throw trapping, we tested the efficiency of the method in two different ways. 1) We released known numbers of both flying and non-flying insects into a previously-placed netted quadrat in order to test vacuuming efficiency. 2) We assessed the contribution of the thrown netted quadrat by sampling a naturally occurring assemblage with and without the netted quadrat.

In the first test, we used crickets, *Acheta domesticus*, and ants, *Formica argentea*, as our subject organisms. The animals were released into the netted quadrats and given an acclimation period as recommended by Hossain et al. (1999) before sampling using our protocol. Fifteen crickets and 25 ants were released into each of four netted quadrats.

In the second test, we assessed the usefulness of the thrown netted quadrat by completing 14 pairs of net/no-net samples using our netted quadrat and a non-netted quadrat. The netted and unnetted quadrats were thrown into the same vegetated habitat and sampled with the vacuum.

Comparisons with pitfall trapping and sweep netting. Despite the efficiency of the vacuum netting technique, there are concerns about using this

protocol in wilderness areas, because the vacuum is a mechanized device. Pitfall traps, sweep netting, and baiting are possible non-mechanized alternatives to vacuum netting. In 2004, we were able to add a comparison of the assemblage characterization provided by vacuum netting versus that determined by pitfall trapping at no cost to NPS (National Science Foundation funding). In 2005, we did paired vacuum net-sweep net samples for comparison.

We established eight replicate matrices of pitfall traps (New 1998) in Devils Postpile National Monument. Each replicate included fifteen individual traps arranged in three rows and five columns with a 1m spacing. Pitfall traps consisted of clear plastic cups, 7.6cm in diameter and 7.6cm deep. The cups were placed in holes of the same dimensions, excavated with a hand trowel, so that the lip of the plastic container was level with the ground. The cores of soil and plant matter from the holes were placed in an area protected from sun and wind. At the conclusion of the study each soil core was returned to its original site.

Pilot studies indicated greater capture during daylight than at night, so we set the 120 traps on thirteen different days in July and August of 2004. A six-hour sampling period was used for each of these trap sets. After six hours all captured fauna were identified to order and released.

We did sweep net comparisons in May-August 2005. The sweep net (New 1998) was a collapsible device with a 30.5cm diameter aperture (Bioquip #7112CP). Twelve paired comparisons were in Tuolumne, and twelve were in the Giant Forest. For each comparison, the vacuum net was first tossed and staked, followed by sweep netting the nearby area. We sweep netted a 200 square meter area on the side of the netted quadrat opposite from the area traversed on our approach to the site. Fifty sweeps were made in a figure-eight fashion throughout the sampling area. Samples were collected by inverting the net into a re-sealable plastic bag. Each sample was placed on ice as soon as possible, although field logistics dictated that some samples were kept in a backpack for several hours before transfer to a cooler or freezer. After sweep netting, the vacuum net sample was collected via the methods outlined above.

Vegetation and physical parameters. Potential predictor variables sampled with each throw trap and/or vacuum net included the following: gram dry mass of both standing crop and litter, canopy height, litter depth (added in 2005), gross percent cover estimates, vegetation dominants, percent cover by plant species, overall patch size (defined by dominant vegetation), water or air temperature, relative humidity (added in 2005), wind speed (added in 2005), soil penetration pressure, soil moisture, water depth, water flow (added in 2005), and water table depth (Tuolumne only). A photo of each plot was also

taken for reference. Faunal response variables included: overall abundances, abundances by order and family, biomass, and morphospecies richness.

After each throw trap or netted quadrat was thrown and sampled, we randomly established the following: two 12.5 cm² standing crop quadrats at each of two outside corners of the faunal sampling device (Fig. 10), a 50 cm² quadrat for characterizing the vegetation assemblage at a third outside corner (Fig. 10), and a Kelway soil moisture meter was sunk into the soil at the remaining corner (2004 terrestrial samples only).

Standing crop and litter were clipped from the two 12.5 cm quadrats (Fig. 10) and dried at 90° C for 24 hours prior to weighing. Percent cover by plant genus or species was recorded for all vascular plant types in the 50 cm² quadrat, and phenological status was noted for each of these taxa. Litter depth was measured with a 1mm diameter spring steel wire.

We recorded soil penetration pressure (kg/cm²) at all four corners of the netted quadrat with a Lang penetrometer with a 0.18 cm² tip. Relative humidity and wind speed were measured with a Kestrel 3000 digital meter. In 2004, percent soil moisture readings were taken at one corner of the netted quadrat with a Kelway meter and at all four corners with a Turf-Tec meter. We found both moisture meters to be unreliable, so in 2005 we began determining soil moisture via gravimetrics as per American Society for Testing and Materials

standards (1992). Each soil sample was composed of 40cc of soil derived in equal parts from surface material at each of the four corners of the fauna plot. Samples were dried at 90° C for 24 hours, and percent water content was determined as follows: *Percent water content*=

$$(1 - ((\text{Mass of dry specimen}) / (\text{Mass of wet specimen}))) \times 100$$

Water flow was measured with a Marsh-McBirney 201 flow meter; we suspended the sensor with a rod held upstream of the observer, and the sensor was maintained in the middle of the water column. We made a rough estimate of water table depth in Tuolumne by measuring depth to water in a standpipe on the north edge of the meadow near the settling ponds.

Fauna were dried at 90° C for 24 hours prior to weighing for biomass estimates.

Analysis. Sign tests, t-tests, ANOVAs, and simple (for initial data exploration) and multiple linear regressions (all possible regressions) were performed in SYSTAT. Family and species richness were corrected using Margalef's index: $(S - 1) / \ln N$ (where S = number of species and N = number of individuals; Clifford and Stephenson, 1975, Magurran 1988). Data were generally log transformed prior to analysis in order to meet assumptions of normality and homogeneity of variance. Many zero and near-zero values occurred, so we used the log+1 transformation. Because of potential collinearity

in the multiple regression models, p to enter the models was set at <0.025 and tolerance was set at 0.1. Even so, multiple linear regression models should be interpreted conservatively.

Results

Vacuum net efficiency. In the test in which fauna were released into the netted quadrat, cricket recapture was 100% (SE= 0%, n=4). Ant recapture was 92% (SE= 2.8%, n= 4).

More fauna were collected in the net samples than in the no-net samples (mean= 125 versus 107 individuals/m²; SE= 35.7 and 42.7, respectively; Fig. 11), but this difference was not significant (one-tailed paired t-test, p= 0.12). Differences were greater, and significant, when individuals capable of flight were considered in isolation (mean net= 54.0 individuals/m², SE= 12.1; mean no-net= 24.4, SE= 6.65; p=0.00039; Fig. 11). Similarly, total species richness did not differ (mean net= 12.7 species/0.25m², SE= 1.13; mean no-net= 11.4, SE= 1.16; p=0.10; Fig. 12), but “flying” species richness was significantly greater in the netted quadrats than in the non-netted quadrats (mean net= 5.86 species/0.25m², SE= 0.417; mean no-net= 4.79, SE= 0.505; p=0.030; Fig. 12).

Vacuum netting versus pitfall trapping or sweep netting. Comparisons of assemblage structure revealed by vacuum netting, pitfall trapping, and sweep netting were necessarily by percentage composition (Figs. 13-15), because pitfall traps and sweep netting do not provide faunal densities. Pitfall traps (Fig. 13) failed to collect flying fauna, including the two dominant taxa, Diptera (flies)

and Homoptera (leafhoppers). Pitfall trap samples were instead dominated by Hymenoptera (ants), Acari (mites), and Araneae (spiders).

Sweep netting (Fig. 14, 15) generally yielded inverse results relative to pitfall trapping. In Tuolumne (Fig. 14), flying taxa such as Diptera, Homoptera, and Hemiptera (true bugs) were overrepresented relative to vacuum netting, whereas predominantly crawling organisms such as Acari, Hymenoptera (largely ants), and Coleoptera (beetles) were underrepresented. Araneae and Lepidoptera were similarly represented by both methods.

Results from the Giant Forest were somewhat more complicated (Fig. 15). Crawling taxa such as Acari, Coleoptera, and Gastropoda again made up a greater proportion of the vacuum samples than the sweep samples. Flying Homoptera and Hemiptera again were overrepresented in the sweep samples. However, Araneae made up a greater proportion of the sweep samples than the vacuum samples, whereas the inverse held for Diptera. Overall abundances as revealed by sweep netting were much greater in the Giant Forest than in Tuolumne: 7,628 and 640 total individuals, respectively, in twelve samples each. Sweep nets produced little additional variance relative to vacuum samples, and in those few cases, the variance was proportional to the mean.

Faunal assemblage structure: Rank-abundance. Aquatic fauna in Tuolumne demonstrated a high level of dominance at the order level, whereas there was

greater evenness in the Giant Forest (Fig. 16). Diptera was the most abundant taxon in both Tuolumne and the Giant Forest and had high frequencies of occurrence in both locations (ranging from 0.92 to 1.0; Table 4), and Ephemeroptera (mayflies) were uniformly important as well. Plecoptera (stoneflies) was the second most abundant order in the Giant Forest. Substantial numbers of Veneroida (clams) were collected in the Giant Forest, and Basommatophora (snails) were found in both the Giant Forest and Tuolumne. Although Coleoptera were not as abundant as some other orders, frequency of occurrence was high (0.92 in Tuolumne 04, 0.64 in Tuolumne 05, and 0.92 in the Giant Forest).

Similar trends in aquatic rank-abundance were seen at the family level (Fig. 17). Mosquito larvae and pupae (Diptera: Culicidae) and mayfly nymphs (Ephemeroptera: Siphonuridae) were of the greatest importance across years and sites, but mosquitos were less common in the Giant Forest than in Tuolumne (frequencies of 0.92, 0.79, and 0.17, respectively in Tuolumne 04, Tuolumne 05, and the Giant Forest; Fig. 17; Table 4). In the Giant Forest, mosquitos were exceeded in abundance by Siphonuridae, Nemouridae (another mayfly family), Simuliidae (blackflies, Diptera), Chironomidae (midges, Diptera), and Sphaeriidae (clams). In the Giant Forest, chironomids, rather than culicids, had a high frequency of occurrence (0.92; Table 4). The Giant Forest had

about twice as many aquatic families (27) as Tuolumne. These family richness trends continued to hold after Margalef's correction for differential abundance (D_{Mg} = 3.3, 1.5, and 1.2 for the Giant Forest, Tuolumne 04, and Tuolumne 05, respectively). Aquatic family richness was highest among the flies, beetles (Coleoptera), and mayflies. Bibionids (March flies, Diptera) were absent in 2005. Excepting the bibionids, the most abundant four families were present in the same ranking in Tuolumne in 2004 and 2005: Culicidae, Siphonuridae, Chironomidae, and Dytiscidae (predaceous diving beetles, Coleoptera; Fig. 17).

Terrestrial trends at the order level demonstrated an inverse pattern to that observed for the aquatics: there was greater evenness in Tuolumne and greater dominance in the Giant Forest (Fig. 18). Abundant orders included Diptera, Homoptera, Araneae, Acari, Coleoptera, and Hymenoptera. Despite the high level of dominance at the Giant Forest, a number of orders had high frequencies of occurrence: Diptera (frequency = 1.0), Homoptera (1.0), Coleoptera (0.98), Araneae (0.94), and Hemiptera (0.90; Table 5).

Terrestrial rank-abundance patterns were similar at the family level: greater evenness in Tuolumne and greater dominance in the Giant Forest (Fig. 19). Formicidae (ants) and Cicadellidae (leafhoppers) were the most common and second-most common families, respectively, in Tuolumne in 2004 (Table 5). In 2005, Sphaeroceridae (Diptera), Formicidae, Linyphiidae (Araneae), and

Cicadellidae were the most common families (in descending order; Fig. 19, Table 5). With a mean of 1,481 animals per square meter, sphaerocerids clearly dominated the Giant Forest and were collected in every sample (Fig. 19; Table 5). Cicadellidae and Drosophilidae (pomace flies) were also common in the Giant Forest and had high frequencies of occurrence (1.0 and 0.83, respectively; Table 5). There were 91 families in our Giant Forest collections; Tuolumne family richness was consistent with 55 families in 2004 and 56 families in 2005; (Fig. 19; Table 5). Correcting for abundance yielded similar adjusted family richness (D_{Mg} = 7.8, 6.9, and 6.7 for the Giant Forest, Tuolumne 04, and Tuolumne 05, respectively). The greatest family richness (Table 5) was found among the flies (Diptera), and beetles (Coleoptera) with 29 and 20 families, respectively.

Faunal assemblage structure: Abundances, frequencies, and species richness: Invertebrate abundances were high in all habitats; we sorted and identified 45,315 individuals in the main study. Among all meadow types and habitats, abundance was highest in the Giant Forest in dry portions of the meadows (mean = 2,267 individuals/m²), these habitats supported over ten times as many animals as the ponded portions (Fig. 20), and the montane Giant Forest meadows had higher abundances across both aquatic and terrestrial habitats (2x2 ANOVA, $p < 0.0001$). Frequencies of occurrence were very high

for some groups (Table 5). The opposite occurred in Tuolumne, where flooded habitat (mean= 884 individuals/m²) harbored over ten times as many fauna as the dry portions (Fig. 20; 2x2 ANOVA, interaction $p < 0.0001$). The montane meadows in the Giant Forest had much greater mean standing crop and mean canopy height than subalpine Tuolumne Meadows (Tables 6, 7). After taking these strong vegetation differences into account, the general abundance trends still remained (Fig. 21, 22; 2x2 ANOVA, interaction $p < 0.0001$ in each case), although the differences in aquatic means were enhanced, and the differences in terrestrial means were reduced. However, overall subalpine-montane comparisons were no longer significant when examining abundance as a function of standing crop (2x2 ANOVA, $p = 0.71$) and canopy height (2x2 ANOVA, $p = 0.97$). The flooded-dry habitat differences (Fig. 23; 2x2 ANOVA, $p = 0.0004$) in Tuolumne were somewhat greater in 2004, a relatively dry year, than in 2005, a relatively wet year (Fig. 23; 2x2 ANOVA, interaction $p < 0.0001$).

Abundances and frequencies for individual aquatic taxa in Tuolumne showed mixed trends across 2004 and 2005 (Table 4). Ephemeroptera, Coleoptera, and Trichoptera all decreased in 2005, although mayfly frequencies remained stable. Falling beetle abundances were the result of reductions in all three collected beetle families: Dytisidae, Hydrophilidae (water scavenger beetles), and Hydraenidae (minute moss beetles). In contrast, there were

increases in damselflies (Odonata: Zygoptera) and true bugs, the latter a function of increases in both collected families: Corixidae (water boatmen) and Notonectidae (backswimmers). Other orders, notably the dominant Diptera showed no change of the two years. Remarkably, the most common family, Culicidae, had a mean of 675 animals per square meter in both years. However, Bibionidae (March flies) were not collected in 2005, and there was an increase in chironomids.

Abundances and frequencies of terrestrial fauna were relatively stable across 2004-2005 in Tuolumne (Table 5). Exceptions at the order level included increases in flies and spiders, and a decrease in mites. Much of the order level increase for Diptera was driven by increases in Sciaridae (root gnats), Lonchopteridae (spear-winged flies), Anthomyiidae (similar to small house flies), Ephydriidae (shore flies), and particularly Sphaeroceridae. Increases in Araneae were largely due to increases in Linyphiidae (sheet-web spiders) and Anyphaenidae (wandering hunters), although the abundance of the latter was largely due to one outlier sample. Otherwise, family abundances across all taxa were generally similar between 2004 and 2005. Frequencies of these groups also generally increased, although the frequency of occurrence for mites remained stable while mite densities decreased (Table 5).

Terrestrial and aquatic species richness were similar in Tuolumne, but terrestrial species richness was greater than aquatic species richness in the Giant Forest (Fig. 24; 2x2 ANOVA, interaction $p = 0.0001$). The Giant Forest had greater overall species richness than Tuolumne, and overall terrestrial species richness was higher than aquatic across locations (Fig. 24; 2x2 ANOVA, $p < 0.0001$ and $p = 0.40$, respectively). Trends were similar after species richness was corrected for differential abundance (Fig. 25), although adjusted terrestrial species richness was greater than non-adjusted aquatic species richness for Tuolumne with the result that the interaction term was no longer significant ($P = 0.071$).

There were no clear trends in aquatic abundances in time that emerged across years and sampling locations. In Tuolumne 2004, total numbers increased by almost a factor of three over the month of meadow flooding (Fig. 26). Both Diptera and Coleoptera showed increases, but the most striking increase was in mayflies, which increased from just a few individuals to almost 1,000 per square meter. These trends were apparent at the family level as well (Fig. 27). Diptera and Ephemeroptera were dominated by culicids and siphonurids, respectively, and these families reflected the patterns seen for their respective orders. Dytiscids and hydrophilids demonstrated increases during the wet phase. However chironomids showed little change, and no

bibionids (March flies) were collected during the latter half of the flooded phase. Biomass for common aquatic groups generally paralleled abundance (Fig. 28). In contrast, in Tuolumne 2005, mayflies and beetles increased through the wet phase, but Diptera decreased (Fig. 29). The Giant Forest showed yet another trend, with some increase in Diptera through the wet phase, accompanied by a decrease in mayflies and stoneflies (Fig. 30).

Terrestrial faunal abundances, however, demonstrated consistency across years and sites. There was a striking trend of increasing abundances until midseason, followed by a steady decrease until snowfall (Figs. 31-36). In Tuolumne 2004, this trend was apparent, and significant (one-tailed sign test, $p < 0.01$), across most of the common orders (Figs. 31, 32); Coleoptera was an exception. This trend was even more clear in Tuolumne during 2005 (Figs. 33, 34; one-tailed sign test, $p < 0.0005$) and in the Giant Forest (Figs. 35, 36; one-tailed sign test, $p < 0.0005$), although leafhoppers, mites, and spiders did not entirely fit the general trend. This overall pattern of a steady increase leading to a peak at mid-season, followed by a steady decrease was present to a lesser extent at the family level (e.g., Tuolumne 04; one-tailed sign test, $p < 0.05$; Fig. 37).

Relationships with vegetation and physical factors. In general, differences between the Giant Forest and Tuolumne were substantially greater

than the differences in Tuolumne in 2004 and 2005. There was much more aquatic vegetation structure in the Giant Forest than in Tuolumne, as indicated by measures of bare ground, green cover, canopy height, and live and dead plant biomass (Table 6). Vegetation in the Giant Forest was also more homogenous, as indicated by larger patch sizes than seen in Tuolumne (Table 6). Mean flow in the flooded meadows, although low, was ten times higher than in Tuolumne. Measures in Tuolumne over the two-year study period were comparatively consistent, although there was more vegetation structure present in the 2004 plots than in the 2005 plots, as evidenced by percent bare substrate and live and dead biomass (Table 6).

Similar trends were seen for terrestrial habitat (Table 7). The Giant Forest had less bare ground, greater canopy height, a deeper litter layer, and more live and dead plant biomass (Table 7). In addition, humidity and soil moisture were higher, and wind speed and penetration pressure were lower, than observed in Tuolumne. Measures in Tuolumne were relatively consistent across 2004 and 2005.

Invertebrates responded differently to the various forms of dominant vegetation. The two dominant vascular plants in Tuolumne flooded habitat were the sedge *Carex utriculata* and tufted hairgrass, *Deschampsia cespitosa*. *Carex utriculata* harbored over three times more total individuals than *Deschampsia*

(Fig. 38). This trend was consistent across the three dominant orders. The differential for mayflies was particularly striking, with means of 513 versus 0.76 individuals per square meter in *Carex utriculata* and *Deschampsia*, respectively. In the Giant Forest, cow-bane, *Oxypolis occidentalis*, harbored more Diptera and Plecoptera than *Carex* sp., but *Carex* supported more Ephemeroptera (Fig. 39).

In general, faunal relationships with terrestrial vegetation were somewhat less strong. In Tuolumne, reedgrass, *Calamagrostis muirii*, supported more Acari, Hymenoptera, and Coleoptera than the other dominant, mountain ricegrass, *Ptilagrostis kingii*, but *Ptilagrostis* supported more Diptera (Fig. 40). In the Giant Forest, we collected more Diptera in Poaceae and meadow goldenrod, *Solidago canadensis*, than in *Carex* sp., but there were no other clear trends (Fig. 41).

There is some indication that three less common plant taxa in Tuolumne dry habitats may harbor even more fauna. *Antennaria* sp. (pussy-toes), *Carex utriculata* (terrestrial samples only), and *Deschampsia cespitosa* produced several times more fauna than *Calamagrostis* or *Ptilagrostis* (Fig. 42), although the former three taxa were only dominant in two, four, and five sampled patches, respectively.

We used simple linear regressions for initial data exploration. Bearing in mind the potential for collinearity, these regressions and associated scatter

plots and 95% intervals intuitively illustrate typical relationships between predictors and faunal abundances. For example, six abiotic and coarse vegetation parameters had a significant influence ($p < 0.05$) on total arthropod abundance in Tuolumne 2004 dry samples. Percent green cover (Fig. 43), green biomass (Fig. 44), total percent cover (Fig. 45), and canopy height (Fig. 46) were positive predictors, whereas soil penetration pressure (Fig. 47) and percent brown cover (Fig. 48) were negative predictors. Percent green cover and penetration pressure appeared to have the most influence across taxa, and demonstrated significant relationships for four out of six tested faunal response variables (Acari, Diptera, Araneae, and total individuals, but not Hymenoptera or Coleoptera).

Multiple regression analysis indicated that several abiotic and coarse vegetation parameters had a significant influence (" p " < 0.025) on arthropod response variables in Tuolumne wet samples (Table 8). There were approximately the same number of negative and positive predictor variables. Water depth and litter mass had the most influence across taxa. (Table 10). Water depth was generally a negative predictor, and litter mass was generally a positive predictor. Some models explained a great deal of the variance in abundances, for instance, 98% and 99% for mayflies and caddisflies, respectively (Table 10). However, no predictors could be entered into models

for Hemiptera or Acari. Percent cover of individual plant taxa (Table 11) did not greatly influence aquatic order densities. Only Odonata abundances were significantly influenced by a plant species (*Carex utriculata*). Linear regressions of aquatic faunal abundances on plant species richness yielded no significant relationships. Simple linear regression of faunal species richness on plant species richness was similarly non-significant ($p = 0.43$).

Coarse physical and vegetation parameters had less influence on Giant Forest aquatic fauna (Table 12) than was seen in Tuolumne. No predictor influenced more than a single taxon. Four predictors were entered into the model for Hemiptera ($R^2 = 0.99$). Predictors could not be entered into models for many taxa. Of the plant taxa found in ponded areas of the Giant Forest (Table 13), only *Carex nebrascensi* (Nebraska sedge) influenced fauna, with a positive coefficient for both Diptera and Gastropoda abundances. Plant species richness was a positive predictor for a single faunal taxon (Odonata; linear regression, $p = 0.0066$), but plant species richness did not affect faunal species richness (linear regression, $p = 0.19$).

Terrestrial arthropod abundances in Tuolumne, with the exception of Coeloptera and Hymenoptera, were influenced by measured coarse physical and vegetation parameters (Table 14), although the R^2 values were lower than for the aquatic models, and fewer predictors were entered into the models. All

predictors were positive, and soil moisture showed the most overall influence, being entered into models for three taxa. Of the plant taxa recorded in dry habitat in Tuolumne (Table 13), only two plant taxa influenced fauna abundance models (Table 14). However, these two taxa, *Antennaria* sp. and *Carex utriculata*, were entered as positive coefficients into models for most taxa; there were no negative coefficients. Neither of the two most common dominants, *Calamagrostis* and *Ptilagrostis*, appeared in any of the models. Plant species richness did not yield significant simple linear models for any faunal taxa, and faunal species richness was not predicted by plant species richness ($p = 0.97$).

Multiple regression models based on coarse physical and vegetation metrics were able to be constructed for all faunal orders in the Giant Forest with the exception of Lepidoptera (Table 17). Most coefficients were positive. Values for R^2 were lower than for the aquatic fauna in the Giant Forest, and fewer predictors were entered into the models. Canopy height was the greatest contributor across taxa (five models). Dry habitat vegetation (Table 16) influenced fauna, with the majority of tested predictors being retained in models (Table 17). All coefficients were positive. Poaceae (grasses) and *Scirpus microcarpus* were incorporated into eight and four models, respectively. Plant species richness was a significant negative predictor of Hemiptera and

Homoptera ($p = 0.028$ and 0.037 , respectively), but did not influence faunal species richness ($p = 0.15$).

Discussion

Vacuum net efficiency and alternative field techniques. The thrown netted quadrat more efficiently captured flying insects and, in conjunction with the vacuum, resulted in a technique for sampling alpine meadows that is analogous to the throw trap in quantitative efficiency. The result is a technique that yielded densities rather than catch-per-unit-effort data. The vacuum net efficiently captured both crawling and flying taxa.

The utility of the vacuum net in capturing flying taxa and producing density data stood in contrast to the results obtained for the pitfall traps. Pitfall traps also disturb the substrate, and raise archaeological concerns. However, the ground-dwelling fauna that were effectively sampled are arguably particularly useful vital signs (see below). Conversely, sweep netting generally yielded fewer crawling taxa relative to vacuum netting. There were two exceptions from the Giant Forest: spiders were collected in greater numbers by sweep netting, whereas we collected more Diptera by vacuuming. Spiders may be easily collected by sweeping because these animals are often found high in the canopy. The decreased *proportion* of Diptera present in the sweep samples in the Giant Forest, relative to Tuolumne, may be due to the large number of the other dominant flying taxon, Homoptera, present in the Giant Forest.

Vacuums clearly have advantages relative to sweep netting including greater efficiency (e.g., Dietrick et al. 1960, Arnold et al. 1973, Buffington and Redak 1998), particularly for ground dwellers (New 1998) and for use in vegetation (Stewart and Wright 1995), as well as reduced damage to organisms (Callahan et al. 1966). Despite the general trend of reduced collection of crawling taxa, sweep nets do have advantages. The apparatus is light in weight, easily transportable, easily demonstrated to field crews, avoids wilderness restrictions, integrates collection over a wider area than vacuum netting, produces samples that require little sorting, and provides reproducible data with variances that are no higher than those produced by vacuum netting. Sweep nets can also be used in areas that are heavily saturated but not flooded. These habitats, which were common in the Giant Forest, are not sampled well by the vacuum and yet cannot be sampled with aquatic techniques. Although ground dwellers are not sampled as well as with vacuum netting, these animals did appear in our sweep net samples. Sweep nets have been shown to yield higher numbers of individuals, species, families, and orders, and capture higher levels of diversity than pitfall traps, light traps, or scented traps (Gadagker et al. 2000). Sweep nets have been used in other Park Service monitoring programs (e.g., in Channel Islands National Park; Fellers and Drost 1991).

Baiting (Bestelmeyer et al. 2000, Delabie et al. et al. 2000) is another option if ants are to be targeted as vital signs (Alonso 2000, Andersen and Majer 2004), as planned, and the vacuum net were to be viewed as an untenable option. Like sweep netting, baiting has the advantage of integrating collection over a larger area than vacuum sampling, although relatively few taxa are sampled well by this technique. We will do field comparisons between baiting and vacuum netting in 2006 as an inexpensive add-on to another project that we are pursuing in Tuolumne.

Although throwtrapping yields high-quality density data and captures rapidly moving taxa well, use of a D-frame dipnet (Merritt and Cummins 1996, U.S. EPA 2002, Hoffman et al. 2005) may prove to be a superior device for the Vital Signs program. The D-frame net is used in a similar fashion to the terrestrial sweep net, and like sweeping and baiting, this technique serves to integrate a relatively large area (U.S. EPA 2002). These nets produce samples with relatively high species richness, comparable to box samplers (Kaminski 1981, Cheal et al, 1993, U.S. EPA 2002) and can collect more taxa than corers, artificial substrates, or activity traps (U.S. EPA 2002, Helgen et al. 1993). These samples can be collected quickly by experienced crews (U.S. EPA 2002, Hoffman et al. 2005) and are lighter and more transportable than throwtraps, and like sweep nets, are easy mastered by field crews. We advocate

comparative sampling of D-frame nets and throwtraps as soon as possible, hopefully achieving cost savings by incorporating this sampling with other work in progress.

Faunal assemblage structure and relationships with vegetation and physical factors. The invertebrate fauna found in these subalpine and montane meadows includes tremendous trophic and autecological diversity (Table 18). Coarse trophic levels range from 1° to 5° consumers, with specialties varying from fungi to honeydew to carrion to spider eggs. The ability to capture so much of the ecosystem's trophic web with a single monitoring tool is one of the great appeals of using invertebrates as a component of the meadow vital signs program.

The low family-level diversity in the flooded meadows relative to dry habitats was probably in part due to the ephemeral nature of the habitat. For instance, Siphonuridae may be the only mayfly family capable of rapidly exploiting the ponds in Tuolumne. In turn, some of the increased aquatic family richness in the Giant Forest may have been due to the presence of sheet flow at 90% of the sampling sites (vs. 21% of the Tuolumne sites) as well as ten times greater mean flow (Giant Forest: 0.038 m/s, SE= 0.14; Tuolumne: 0.0036 m/s, SE= 0.0022). Although both mean flow rates are low, the difference was visually apparent, and the flow present at the Giant Forest likely represented

increased habitat diversity relative to Tuolumne and may have been responsible for the abundance of arthropod taxa such as Nemouridae and Simuliidae as well as clams and snails. This flow may have also contributed to the reduced presence of mosquitos in the Giant Forest.

The higher terrestrial family richness observed in the Giant Forest was likely a function of several factors including more habitat structure (e.g., canopy height, standing crop), and higher mean soil moisture (Giant Forest: 60%, SE= 3.8; Tuolumne: 42%, SE= 2.4). At some sample locations in the Giant Forest, the soil was completely saturated, to the extent that water was expelled from the vacuum outlet, and live bivalves were collected. The longer growing season in the Giant Forest may have been a factor as well, although on a year-to-year basis growing season duration had no effect on Tuolumne species richness (55 families in 2004 vs. 56 in the shorter season of 2005).

Overall, the two years of sampling in Tuolumne indicated a relatively stable community structure. This consistency bodes well for the monitoring plan, as these results suggest that a good signal-to-noise ratio could be expected. The most notable change among the Tuolumne aquatic fauna between 2004 and 2005 was the disappearance of bibionid fly larvae in 2005. In 2004, bibionids disappeared from the wet samples after the first two weeks, and the larvae observed during the first two weeks were often dead or

senescent. The Bibionidae are also known as March Flies, because reproduction and general activity are concentrated in the spring (Hardy 1981). It may be that there is a thriving bibionid population, including both larvae and adults, under the snow in late spring that is subsequently flooded during melt-off. In 2005, with melt-off occurring a month later (June) than in 2004, the March flies may have flourished and vanished prior to our sampling.

Another minor change over the two years of sampling in Tuolumne was an increase in large predators such as backswimmers and damselflies, although the numbers of these organisms was not high. The long wet winter of 2005 resulted in a long period of standing water in Tuolumne, and this longer wet phase may have allowed populations of large invertebrate predators to develop. In turn, the increased number of predators could have led to the observed decrease in mayfly abundance during 2005.

In the subalpine meadows at Tuolumne, taxa that made use of the ephemeral flooded resource reached high densities. Aquatic densities were ten times greater than terrestrial densities over the entire season, and this differential was particularly pronounced in early season. Flooded meadow habitat is likely to account for a majority of the annual meadow invertebrate production in a given summer, despite persisting for only one to two months. High aquatic, relative to terrestrial, abundances also occurred in meadow habitat

in nearby Devils Postpile National Monument in 2002-2004 (Holmquist and Schmidt-Gengenbach 2005).

The opposite pattern was observed in the Giant Forest, where terrestrial abundances and species richness were high, likely as a result of many of the factors put forward above as possible explanations for the high family richness found in these meadows. The differences in terrestrial abundance between the Giant Forest and Tuolumne were reduced after taking into account the taller canopy height and greater standing crop in the Giant Forest.

Terrestrial fauna showed remarkably consistent two- to three-fold increases in population densities until mid-season, across all sites and years. By the end of the growing season, terrestrial abundances dropped significantly to about one-fifth of the levels observed at mid-season. These early-mid season versus late season trends were also observed in Tuolumne Meadows, Dana Meadows, May Lake, and Yosemite Valley during 2001-2002 (Holmquist and Schmidt-Gengenbach 2004) and in Devils Postpile during 2002-2004 (Holmquist and Schmidt-Gengenbach 2005).

Early-mid season meadows represent a remarkably productive resource. Flooded habitat largely disappears after one-two months, and terrestrial abundances reach their maxima two-three months into the season. Early-season meadow habitat is known to be susceptible to grazing impacts, and

management decisions are made with this sensitivity in mind. Given that invertebrate production appeared to be very high in early season and very low in late season, it is possible that invertebrate assemblages are even more sensitive than flora to grazing impacts in early season but more resistant to disturbance in late season. The importance of invertebrates in ecosystem function and the observed high rates of production in early-season meadows should warrant consideration when adopting meadow management practices.

Vegetation appeared to have an influence on aquatic fauna. In particular, *Carex utriculata* produced much greater faunal abundances than *Deschampsia* in the Tuolumne aquatic samples. *Carex utriculata* was also the only plant species that was successfully entered into the multiple regressions for Tuolumne aquatic fauna, although this entry was for a single model only.

Although the influence of dominant terrestrial flora was in general less than was seen in the aquatic habitats, Poaceae and Solidago did produce somewhat greater abundances of fauna in the Giant Forest. Poacea was also successfully entered into regression models for most taxa. In Tuolumne, the two most common dominants, *Calamagrostis* and *Ptilagrostis* did not appear in any models. In contrast, *Antennaria* sp. and *Carex utriculata* appear to support high densities of fauna, although there were only a few quadrats dominated by each of these species. On the other hand, *Antennaria*, while rarely dominant,

was present in 73 of the 94 Tuolumne terrestrial quadrats, and both *Antennaria* sp. and *Carex utriculata* were influential predictors in multiple regressions on terrestrial faunal abundances. These two apparently important plants had remarkably divergent architecture; *Antennaria* forms low mats, whereas *C. utriculata* had the tallest canopy height observed in our Tuolumne samples. It is unlikely that the apparent influence of *Antennaria* was simply indicative of higher plant diversity in the plots containing this species, because regressions of Tuolumne faunal abundances and species richness on plant species richness did not produce significant models. *C. utriculata* was generally a monoculture, so co-occurring taxa would not be an explanation for this species either. Because *C. utriculata* was also an important determinant of both aquatic and terrestrial faunal abundances, this sedge may deserve attention as an important resource.

Invertebrates as vital signs. Numerous ecologists have warned against monitoring managed lands exclusively via plants and vertebrates, and have contended that invertebrates should play an important role as reserve indicators because of the prominent role that these organisms play in ecosystem function (e.g., Refseth 1980, New 1993, Oliver and Beattie 1994). Plant data, though critically important, cannot serve as a proxy for invertebrate assemblage health. “Plants are notoriously poor surrogates of invertebrate biodiversity, so on their own fail to provide an adequate representation of biodiversity and ecosystem

function” (Andersen and Majer 2004). For instance, Kremen (1992) found little concurrence between plant richness and butterfly richness along old trail and road edges. Similarly, Holmquist and Schmidt-Gengenbach (2004) found many fewer invertebrates in disrupted portions of Sierra meadows than in core meadow habitat, despite similar vegetation parameters throughout. Other examples from the terrestrial realm include work by Jonsson and Jonsell (1999), Dangerfield et al. (2003), and Axmacher et al. (2004; see also Axmacher et al. 2006), among others. Analogous results have also been reported from aquatic systems, e.g., Eckrich and Holmquist (2000) and Uhrin and Holmquist (2003).

Clark and May (2002), in a *Science* article, *Taxonomic bias in conservation research*, demonstrated that vertebrates are grossly over-represented in terrestrial conservation and management efforts, whereas invertebrates are poorly represented in such programs. Insects are particularly useful as indicators because of their abundance, species richness, ubiquitous presence, importance in ecosystem function (Holloway 1980, Rosenberg et al. 1986) and are particularly sensitive to disturbance, expressed both by mortality and emigration. Effects are often amplified by insects’ prodigious reproductive potential. Also, the variety of trophic levels represented, even within a given taxon, makes for great indicator sensitivity (Samways 1994). For these reasons, invertebrates will often be better as rapid response “sentinel species”

(New 1995) than vegetation surveyed in isolation. “[Invertebrates] provide a far more fine-grained and dynamic view of ecosystems than do plants. Yet they are uncomfortably foreign to most land managers” (Andersen and Majer 2004). Invertebrate indicators should be an important complement to vegetation monitoring.

Because of this utility, terrestrial invertebrates have been used as indicators throughout the world; a few examples follow. Given the diversity present in neotropical forests, it is not surprising that insects have served as indicators in this system (Brown 1997). Europe has a long history of interest in landscape configuration, and moths, ants, and ground beetles (Carabidae) have been used as indicators of land use change (Eyre et al. 1986, Eyre and Luff 1990, Rushton et al. 1990, Ehrhardt and Thomas 1991, Luff and Woiwod 1995). Ground beetles have a particularly rich history of use (e.g., Stork 1990, Freitag 1979, Pearson and Cassola 1992). Insects have also been used as indicators in evaluating grazing pressure in Germany (Meyer and Hans-Dieter 1996). In Australia, indicators have included grasshopper diversity in Kakadu National Park (Andersen et al. 2001), ant diversity and functional groups on recovering mining sites (Majer 1983, 1995, Majer and Nichols 1998, Andersen 1993, 1997, Andersen and Majer 2004), ant and spider assemblage structure and succession on military and/or grazing land (Woinarski et al. 2002, Schnell et

al. 2003), and leaf litter invertebrates in Barrine National Park (Jansen 1997). Use of invertebrates as indicators in Africa includes dung beetles in a savanna ecosystem in Tembe Elephant Park, South Africa (McGeoch et al. 2002), moths on Mt. Kilimanjaro (Axmacher et al. 2004, 2006), and snails in Madagascar (Emberton 1996). Other groups that have been used with success include Diptera and parasitic Hymenoptera (Disney 1986) and ants and termites (Andersen 1990).

Not all investigated groups have served as good indicators. For instance, Kremen (1992) found butterflies to be good indicators of heterogeneity derived from topographic gradients, but of only limited use for detecting disturbance.

Six characteristics that are desirable for indicators are outlined by Hellawell (1986) and New (1995):

- 1) Reasonable, but not overwhelming diversity
- 2) Well-known taxonomy
- 3) Ease of sampling
- 4) Sufficient abundance for reliable detection of changes in incidence and abundance
- 5) Wide distribution in the target ecosystem
- 6) A mixture of ecological roles in the taxon and knowledge of these roles

New (1984, 1987, 1995, 1996) and Lawton et al. (1998), among others, have advocated assemblage level analyses that incorporate a number of terrestrial functional groups: for instance, Collembola (soil and litter, in decomposer food webs), leafhoppers and chrysomelid beetles (herbivores with differing feeding ecologies), ants (particularly valuable because of wide distribution and diverse trophic interactions), and ground beetles (active predators). A strength of this approach is that many taxa are typically collected via a given field technique, and an assemblage level strategy conserves this information. Many trophic levels are represented, allowing high indicator sensitivity. Similarly, McGeoch et al. (2002) advocate use of detector taxa that represent a broad range of autecologies in order to best anticipate direction of ecological change. Examples of others adopting this approach for terrestrial arthropods include Gadagkar et al. (1990), Owen and Owen (1990), Clark and Samways (1993), Yen and Butcher (1997) and Ward and Larivière (2004). This summer we will be conducting a NPS sponsored study of human trampling effects on subalpine fauna and flora in Tuolumne, and the results of this work should provide an indication of the sensitivity of family-level indicators. Of course, use of aquatic invertebrate assemblages as monitoring tools is well established (e.g., Hilsenhoff 1988, Resh and Jackson 1993, Kerans and Karr 1994, Harig and Bain 1998, Barbour et al. 1999, Hawkins et al. 2000).

We advocate the assemblage/family-level approach for the Sierra Nevada Network, making use of both aquatic and terrestrial taxa, but we also suggest genus and/or species level analyses of ants as a complement.

Ants have had great success as indicator groups in terrestrial systems (e.g., Greenslade 1978, Andersen 1990, 1993, 1997, Alonso 2000, Majer and Nichols 1998, Andersen and Majer 2004). Much of this utility is because ants meet Hellawell's above criteria particularly well. In addition, ants include many specialist taxa and are responsive to changing environmental conditions (Majer 1983, Kaspari and Majer 2000). Erhardt and Thomas (1991) found ants to be three times more responsive to environmental change than the plants with which the formicids were associated. Use of ant genera can be particularly efficient, because these higher-level groups 1) bypass ignorance of species level biology, 2) simplify complex assemblages, 3) provide insights into major processes, and 4) allow meaningful comparisons on a large geographic scale (Andersen 1990).

There is an additional benefit to use of ants as one of a suite of invertebrate vital signs: ants are among the most dangerous invasives that threaten natural systems (New 1995). Almost ten percent of California's 281 ant species are non-native (Ward 2005). Monitoring ants would provide early

detection of destructive exotic species such as the Argentine ant and red imported fire ant that may threaten the Sierra Nevada ecosystem.

We recommend monitoring aquatic and terrestrial invertebrates at the family level, defaulting to order level identifications when necessary for efficiency. We estimate that family identifications can be made rapidly for 80% of collected specimens, and many of these identifications can be made while sorting and without the use of a microscope. We also suggest monitoring ants at the genus and/or species level. The broad family level surveys would provide extensive taxonomic monitoring, whereas monitoring ant populations would provide a good fine-scale response to changing conditions. Such a two-tiered taxonomic approach is currently planned by the Vital Signs program and should prove to be a powerful monitoring strategy.

We think that the program can be implemented most efficiently using three catch-per-unit-effort tools: sweep nets for terrestrial faunal surveys, D-frame nets for aquatic sampling, and baiting for sampling ants. These techniques are currently planned as the devices to be used in the invertebrate monitoring program. We would also recommend very limited sampling using techniques that yield density data as a standard against which to compare the catch-per-unit-effort data that will be more extensively collected. These density-yielding devices would be the throwtrap and vacuum net used in this

study, and a small number of samples using these devices could be collected at easily accessed sentinel sites in non-wilderness areas. We are taking this density + catch-per-unit-effort data approach in our meadow invertebrate monitoring in the White Mountains (Inyo National Forest) as part of the GLORIA program (Global Observation Research Initiative in Alpine Environments; Grabherr et al. 2000). Regardless of which techniques are used in the Sierra Network, our ongoing meadow invertebrate monitoring in the White Mountains should provide valuable data to compare with that generated by the Sierra Nevada Network Vital Signs program.

In the current study, we sampled meadows throughout the growing season in an effort to better understand seasonal dynamics. However, it is most cost effective to monitor invertebrates when abundances are greatest (Samways 2005), and once the monitoring plan is in place, we intend to sample terrestrial invertebrates at the same time that vegetation is sampled, i.e., at the height of the growing season, when invertebrates are most abundant. This measure will cut costs dramatically and thus greatly expand the number of sites that could be efficiently sampled. There is a great deal of flexibility in the entire sampling, sorting, identification, and analysis process, and protocols could easily be adapted to changing monitoring needs.

Although the importance of invertebrates is widely recognized by managers and scientists, there has been a widespread impression that invertebrates are “too hard” (Andersen and Majer 2004, Ward and Larivière 2004) to use as indicators because of perceived sampling and taxonomic difficulties. We believe that these first two years of study, and the literature review in this report and Holmquist (2004), should provide assurance that invertebrates can be efficiently sampled, taxonomy can be manageable, and that there is sufficient signal-to-noise ratio to detect spatial and temporal trends. As noted by Anderson and Majer (2004), invertebrates are too valuable a monitoring toolbox to ignore.

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Figure Captions

Fig. 1. Early, mid, and late season meadow habitat in Tuolumne Meadows, Yosemite National Park. Note flooding and persisting snow in early season.

Fig. 2. Early, mid, and late season meadow habitat in Log and Crescent Meadows, near the Giant Forest, Sequoia National Park. Note flooding and persisting snow in early season as well as stream influence (arrow).

Fig. 3. Locations of twelve aquatic samples (circles) and 48 terrestrial samples (diamonds) in Tuolumne Meadows in 2004.

Fig. 4. Locations of fourteen aquatic samples (circles) and 46 terrestrial samples (diamonds) in Tuolumne Meadows in 2005.

Fig. 5. Locations of twelve aquatic samples (circles) and 48 terrestrial samples (dots) near the Giant Forest. Allocation of terrestrial samples by meadow is indicated by boxed numbers. Samples were dispersed randomly within suitable habitat; Log Meadow had a disproportionate number of terrestrial samples, because this meadow had the greatest proportion of dry habitat.

Fig. 6. Tossing the throw trap into flooded meadow habitat.

Fig. 7. Scooping fauna out of the throw trap and washing the bar seine. P. Moore photos.

Fig. 8. Plankton splitter used to split samples into equal portions.

Fig. 9. Tossing the netted quadrat and vacuuming fauna from vegetation through the elasticized aperture in the net. L. Greene photos.

Fig. 10. Standing crop and assemblage structure quadrats.

Fig. 11. Total number of invertebrates per m² and number of “flying” individuals per m² captured with netted and unnetted quadrats (n= 14). P-values resulted from one-tailed paired t-tests.

Fig. 12. Species richness of total invertebrates and “flying” invertebrates captured with netted and unnetted quadrats (n= 14). P-values resulted from one-tailed paired t-tests.

Fig. 13. Total percent of fauna by order collected by vacuum netting and pitfall trapping. Underlined taxa were represented entirely by flying species.

Fig. 14. Mean (SE) percent of fauna by order collected by vacuum netting and sweep netting in Tuolumne. Underlined taxa were represented entirely by flying species.

Fig. 15. Mean (SE) percent of fauna by order (plus Class Gastropoda) collected by vacuum netting and sweep netting in the Giant Forest. Underlined taxa were represented entirely by flying species. Taxa for which bars are apparently absent were represented by so few individuals that bars are not distinguishable (the same applies in subsequent graphics).

Fig. 16. Aquatic rank-abundance by order. Note different y-axis for the Giant Forest.

Fig. 17. Aquatic rank-abundance by family. Note different y-axis for the Giant Forest.

Fig. 18. Terrestrial rank-abundance by order (plus Class Gastropoda). Note different y-axis for the Giant Forest.

Fig. 19. Terrestrial rank-abundance by family. See Table 4 for family names. Note different y-axes.

Fig. 20. Mean (SE) for number of individuals/m² as a function of meadow type and inundation in 2005.

Fig. 21. Mean (SE) for total abundance per g dry mass standing crop as a function of meadow type and habitat type in 2005.

Fig. 22. Mean (SE) for total abundance per cm canopy height as a function of meadow type and habitat type in 2005.

Fig. 23. Mean (SE) for number of individuals/m² in subalpine (Tuolumne) meadows as a function of habitat type and year. The winter of 2004 was relatively dry, whereas 2005 was a wet year.

Fig. 24. Species richness (SE) in flooded and dry habitat in subalpine (Tuolumne) and montane (Giant Forest) meadows.

Fig. 25. Species richness corrected by Margalef's adjustment (SE) for flooded and dry habitat in subalpine (Tuolumne) and montane (Giant Forest) meadows.

Fig. 26. Mean (SE) for abundance of common aquatic orders for Tuolumne 2004 during the first and second halves of the flooded period (four weeks total).

Fig. 27. Mean (SE) for abundance of common aquatic families for Tuolumne 2004 during the first and second halves of the flooded period (four weeks total).

Fig. 28. Mean (SE) for biomass of common aquatic orders for Tuolumne 2004 during the four weeks in which flooded habitat was present.

Fig 29. Mean (SE) for abundance of common aquatic orders for Tuolumne 2005 during the first and second halves of the flooded period.

Fig. 30. Mean (SE) for abundance of common aquatic orders in the Giant Forest during the first and second halves of the flooded period.

Fig. 31. Mean (SE) for abundance of total terrestrial fauna and Acari, the most common terrestrial order, during the five snow-free months in Tuolumne Meadows 2004.

Fig. 32. Mean (SE) for abundance of common orders (Hymenoptera, Coleoptera, Diptera, and Araneae) during the five snow-free months in Tuolumne Meadows 2004.

Fig. 33. Mean (SE) for abundance of total terrestrial fauna and Diptera, the most common terrestrial order, during the five snow-free months in Tuolumne Meadows 2005.

Fig. 34. Mean (SE) for abundance of common orders (Hymenoptera, Homoptera, Acari, and Araneae) during the five snow-free months in Tuolumne Meadows 2005.

Fig. 35. Mean (SE) for abundance of total terrestrial fauna and Diptera, the most common terrestrial order, during the six snow-free months in the Giant Forest.

Fig. 36. Mean (SE) for abundance of less common orders (Hymenoptera, Homoptera, Acari, Coleoptera, and Araneae), during the six snow-free months in the Giant Forest.

Fig. 37. Mean (SE) for abundance of common families, Formicidae (ants), Cicadellidae (leafhoppers), Chloropidae and Anthomyidae (two fly families), and Ichneumonidae (a wasp family) during the five snow-free months in Tuolumne Meadows 2004.

Fig. 38. Aquatic insect densities in Tuolumne (2004-2005) by dominant vegetation type. *Carex utriculata*, n= 14; *Deschampsia cespitosa*, n= 7.

Fig. 39. Aquatic insect densities in the Giant Forest by dominant vegetation type. *Oxypolis occidentalis*, n= 4; *Carex sp.*, n= 5.

Fig. 40. Terrestrial arthropod densities in Tuolumne (2004-2005) by dominant vegetation type. *Calamagrostis muirii*, n= 30; *Ptilagrostis kingii*, n=40.

Fig. 41. Terrestrial arthropod densities in the Giant Forest by dominant vegetation type. Poaceae, n= 19; *Solidago canadensis*, n= 9; *Carex sp.*, n=8

Fig. 42. Total terrestrial arthropod densities by dominant vegetation type in Tuolumne (2004-2005). *Carex utriculata*, n= 4; *Antennaria sp.*, n= 2; *Deschampsia cespitosa*, n= 5; *Ptilagrostis kingii*, n=40; *Calamagrostis muirii*, n= 30;.

Fig. 43. Linear regression of total terrestrial arthropod densities in Tuolumne 2004 on percent green cover; 95% confidence intervals.

Fig. 44. Linear regression of total terrestrial arthropod densities in Tuolumne 2004 on green biomass; 95% confidence intervals.

Fig. 45. Linear regression of total terrestrial arthropod densities in Tuolumne 2004 on total percent cover; 95% confidence intervals.

Fig. 46. Linear regression of total terrestrial arthropod densities in Tuolumne 2004 on canopy height; 95% confidence intervals.

Fig. 47. Linear regression of total terrestrial arthropod densities in Tuolumne 2004 on soil penetration pressure; 95% confidence intervals.

Fig. 48. Linear regression of total terrestrial arthropod densities in Tuolumne 2004 on percent brown cover; 95% confidence intervals.

Fig. 1

Early season



Mid-season



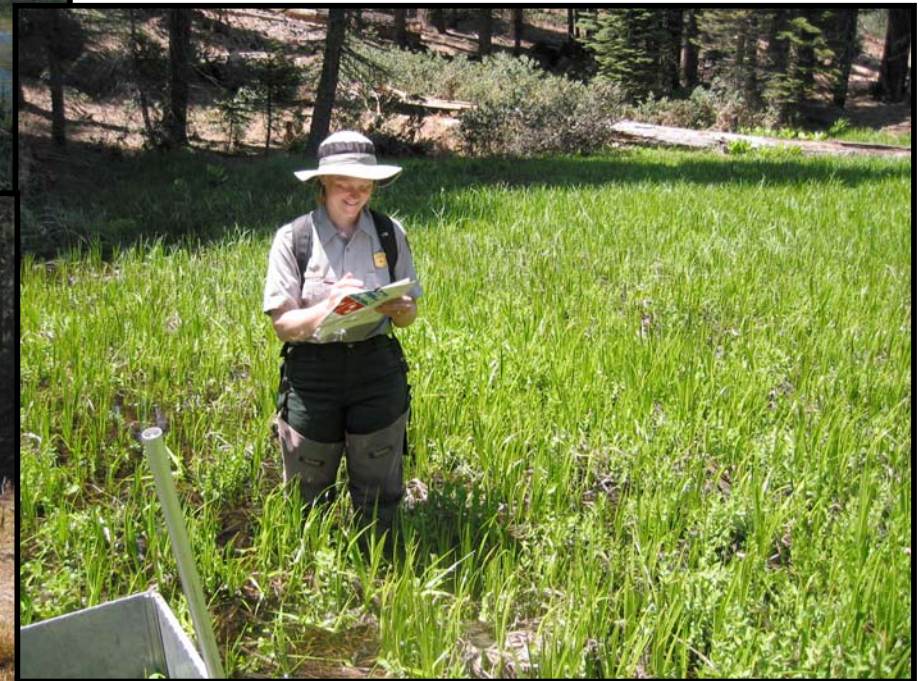
Late season



Fig. 2

Early season

Mid-season



Late season

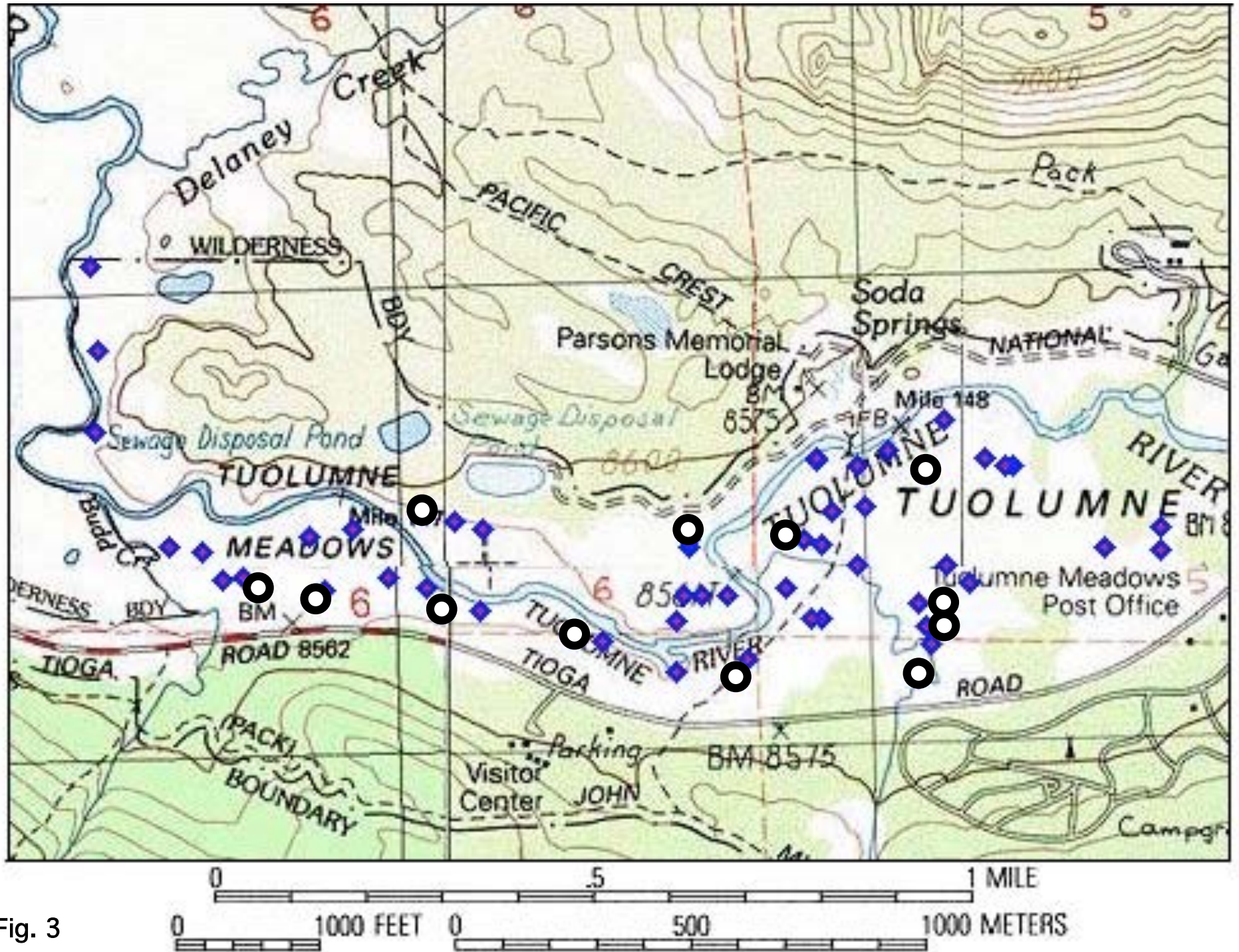


Fig. 3

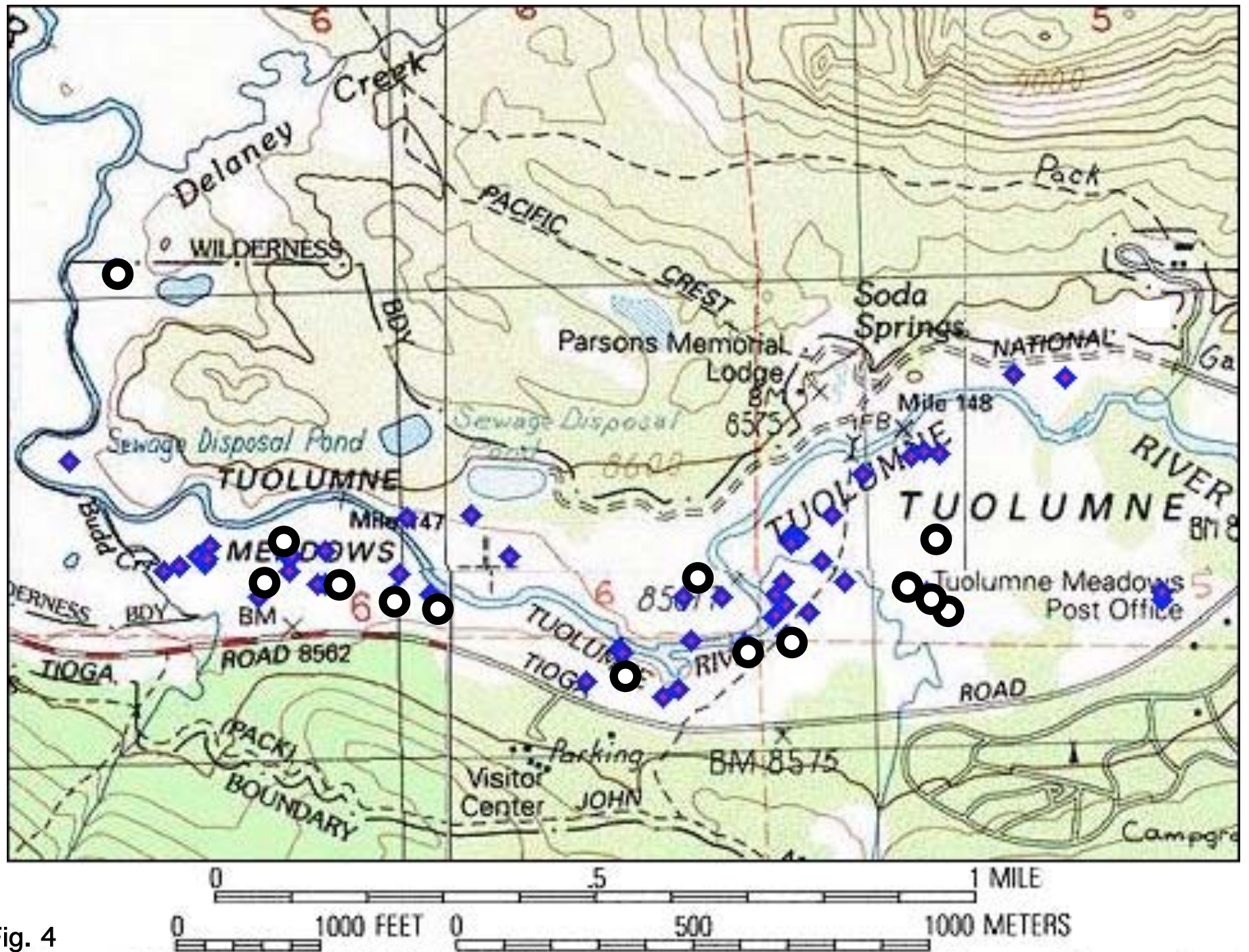


Fig. 4

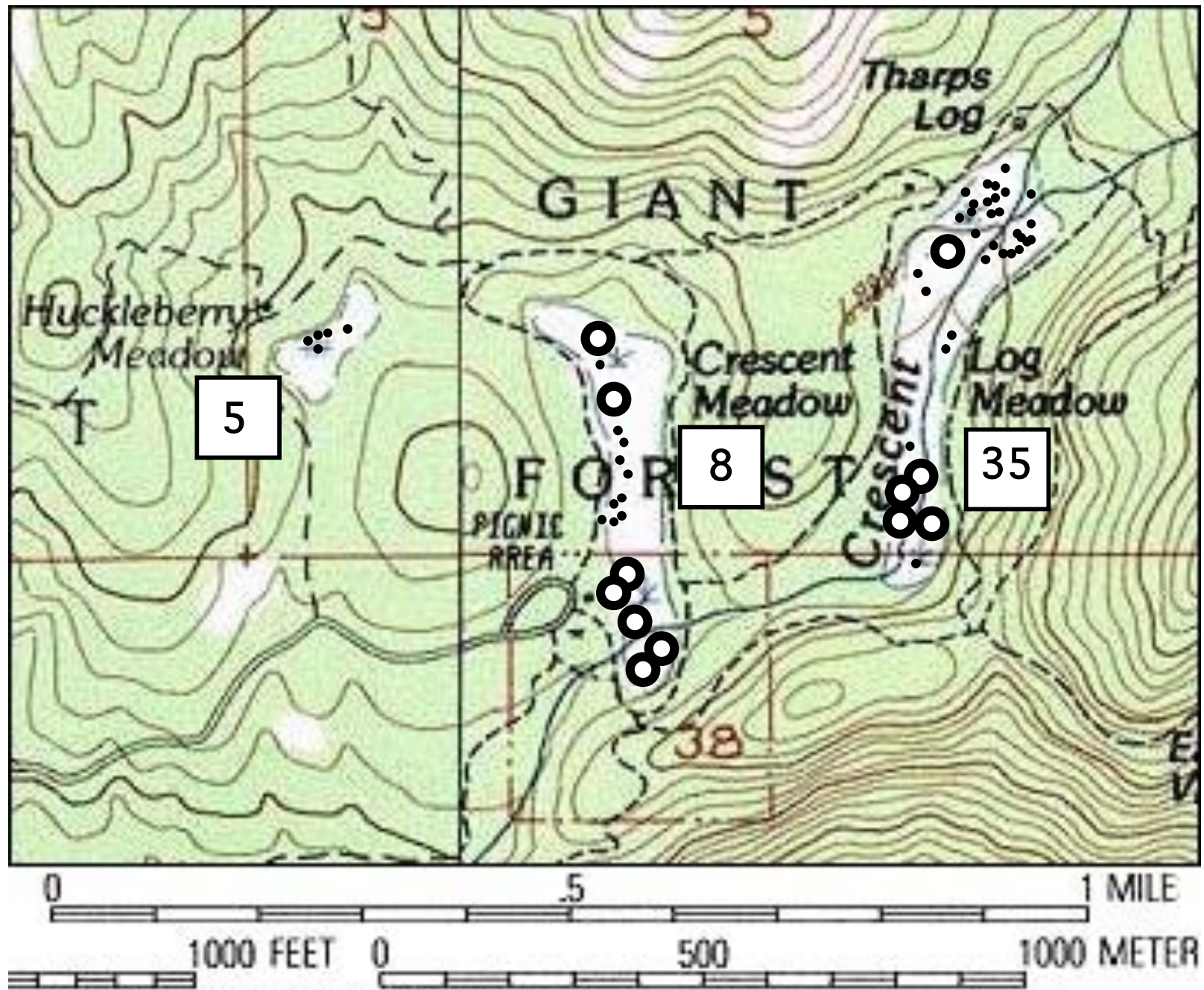


Fig. 5

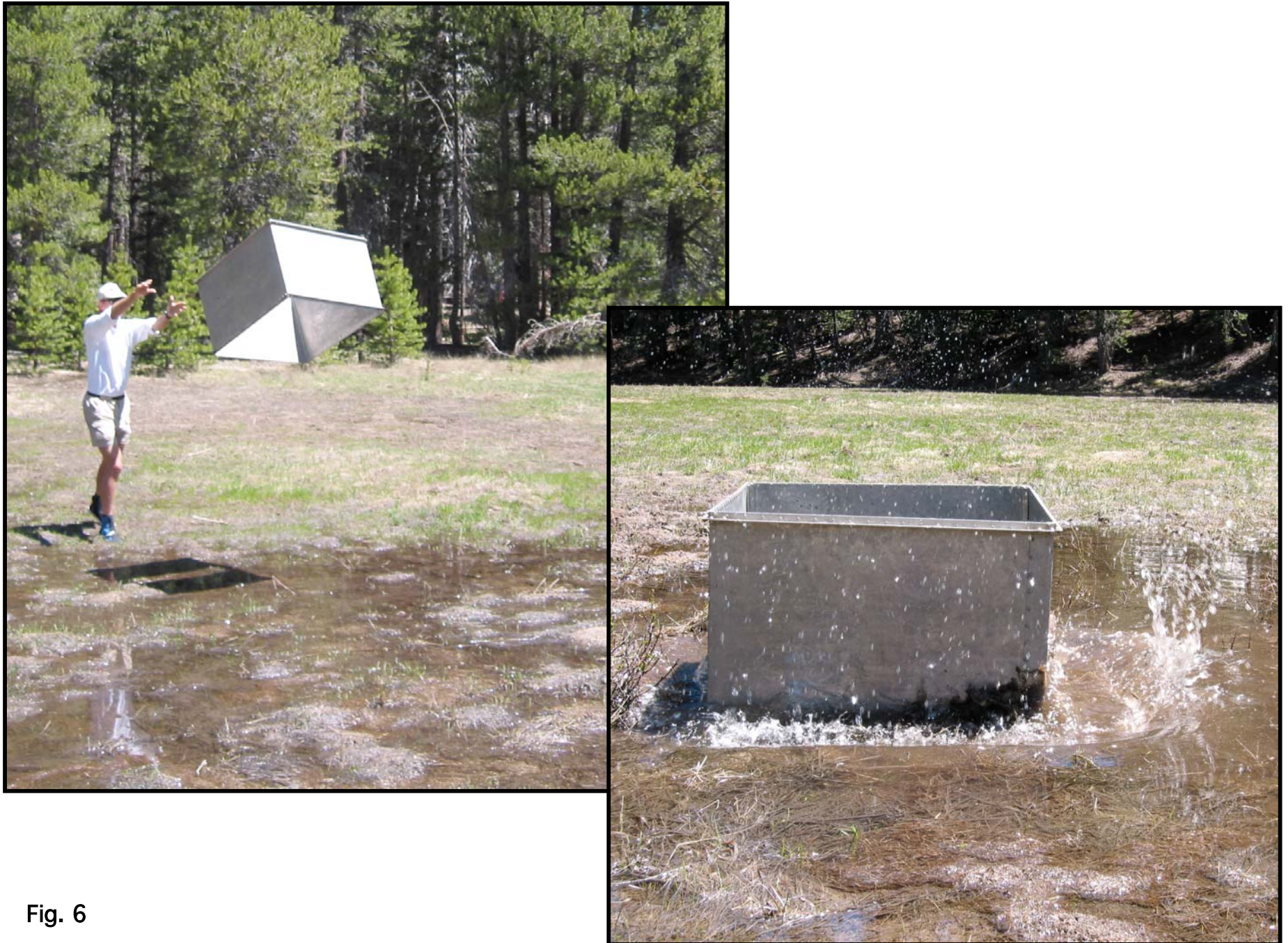


Fig. 6



Fig. 7



Fig. 8



Fig. 9



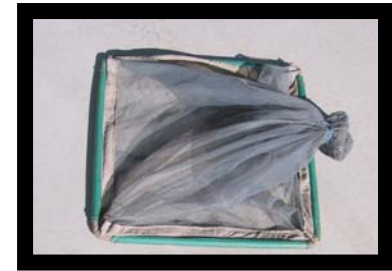
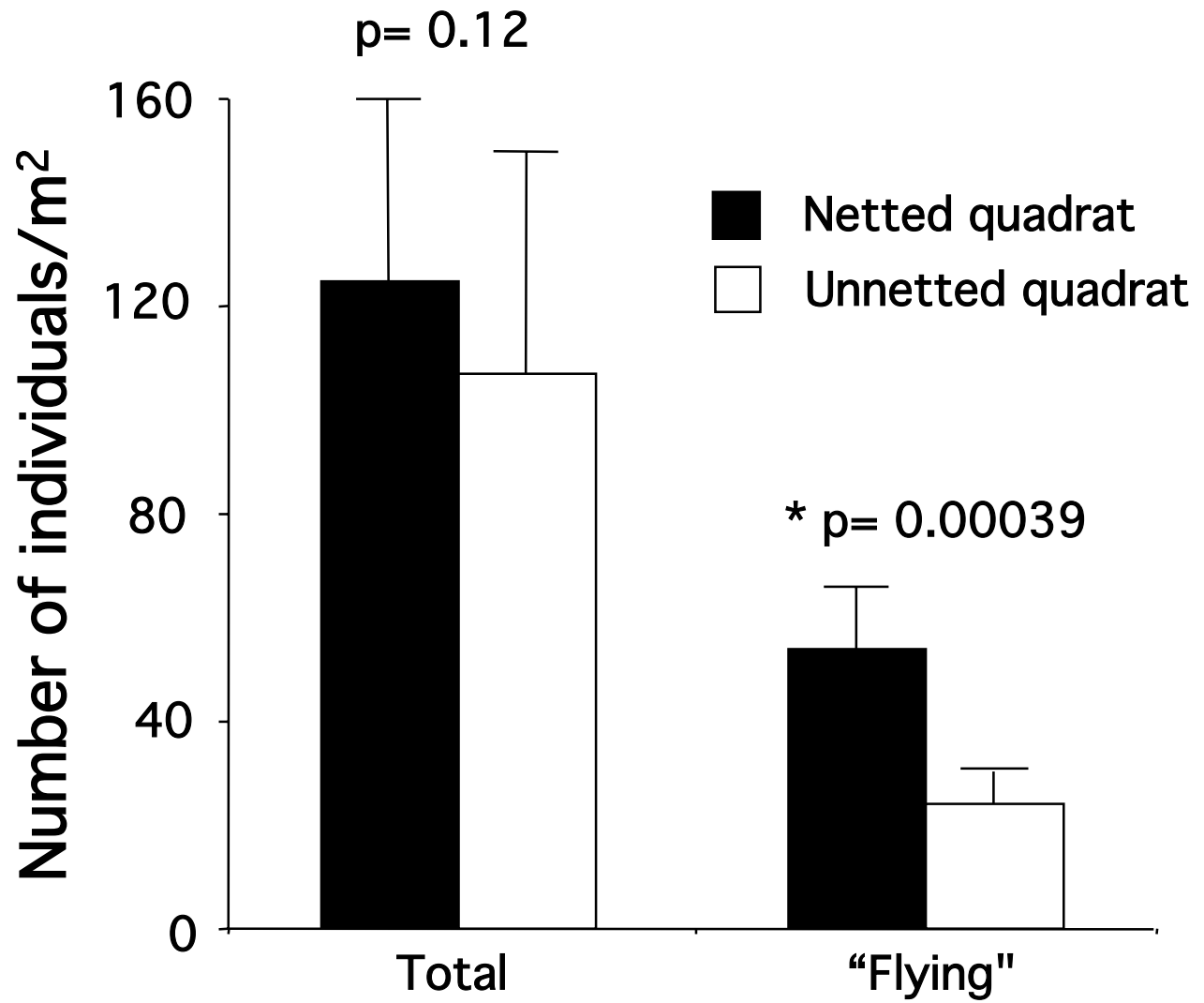
Standing crop

Assemblage structure



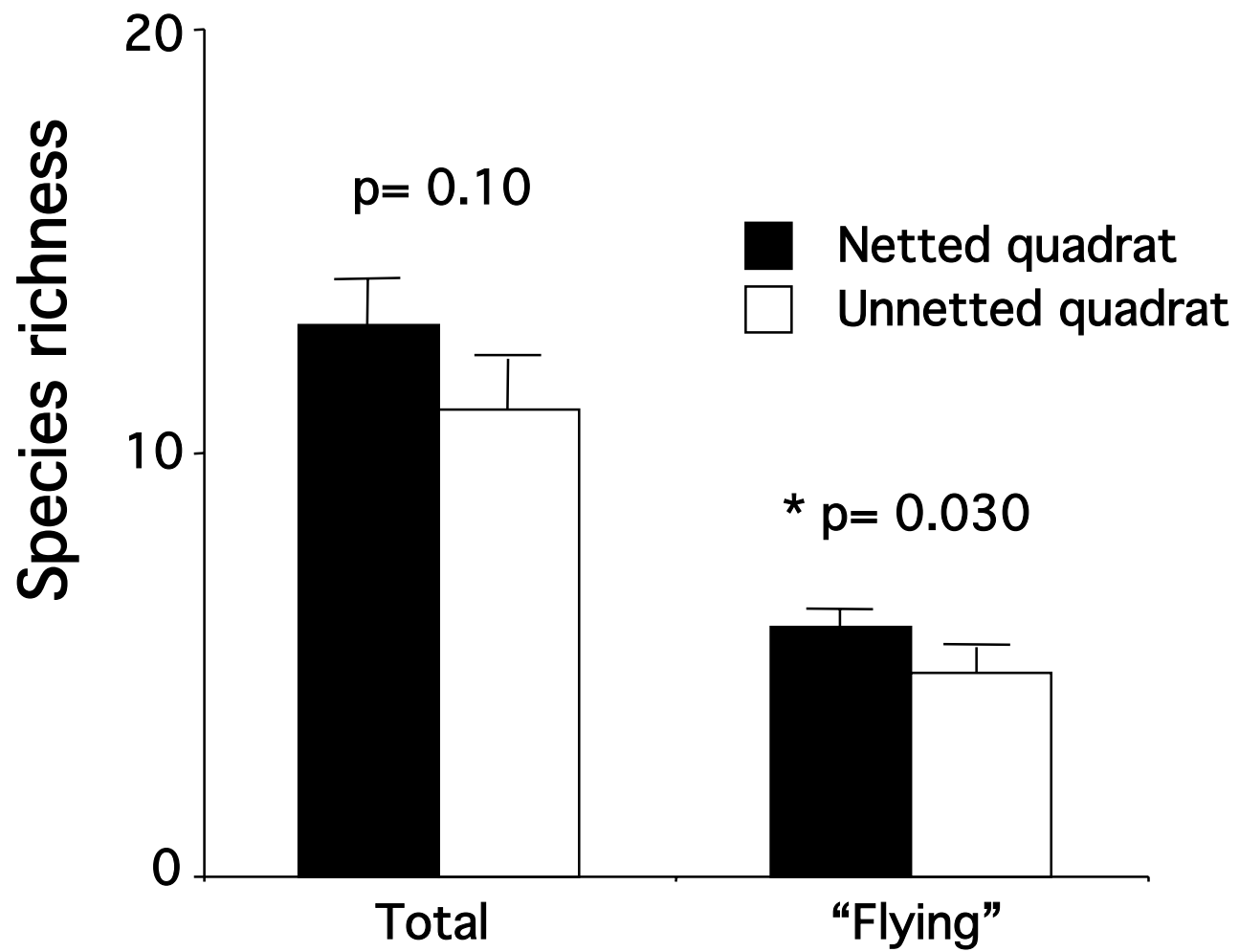
Fig. 10

Fig. 11



n = 14

Fig. 12



n= 14

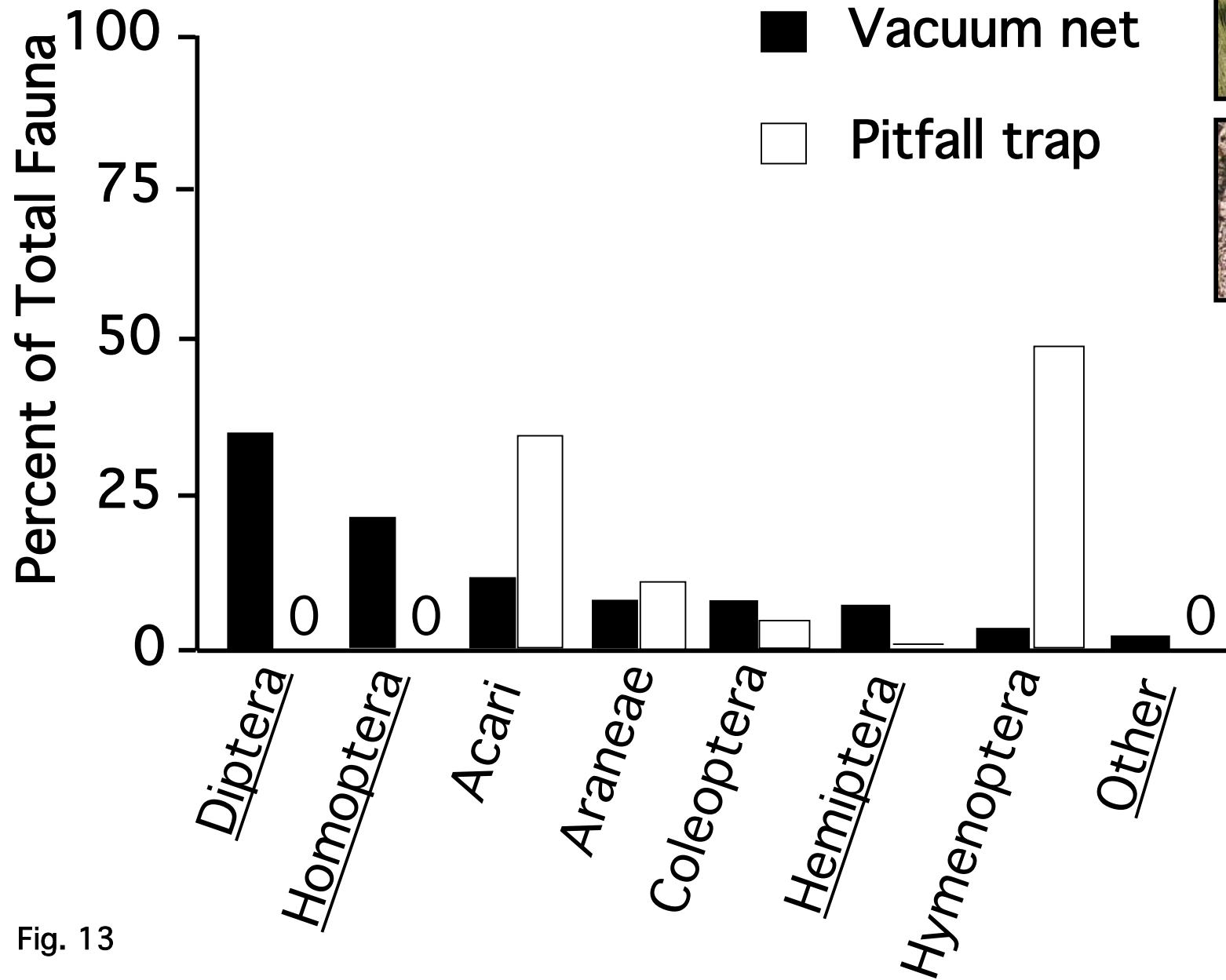


Fig. 13

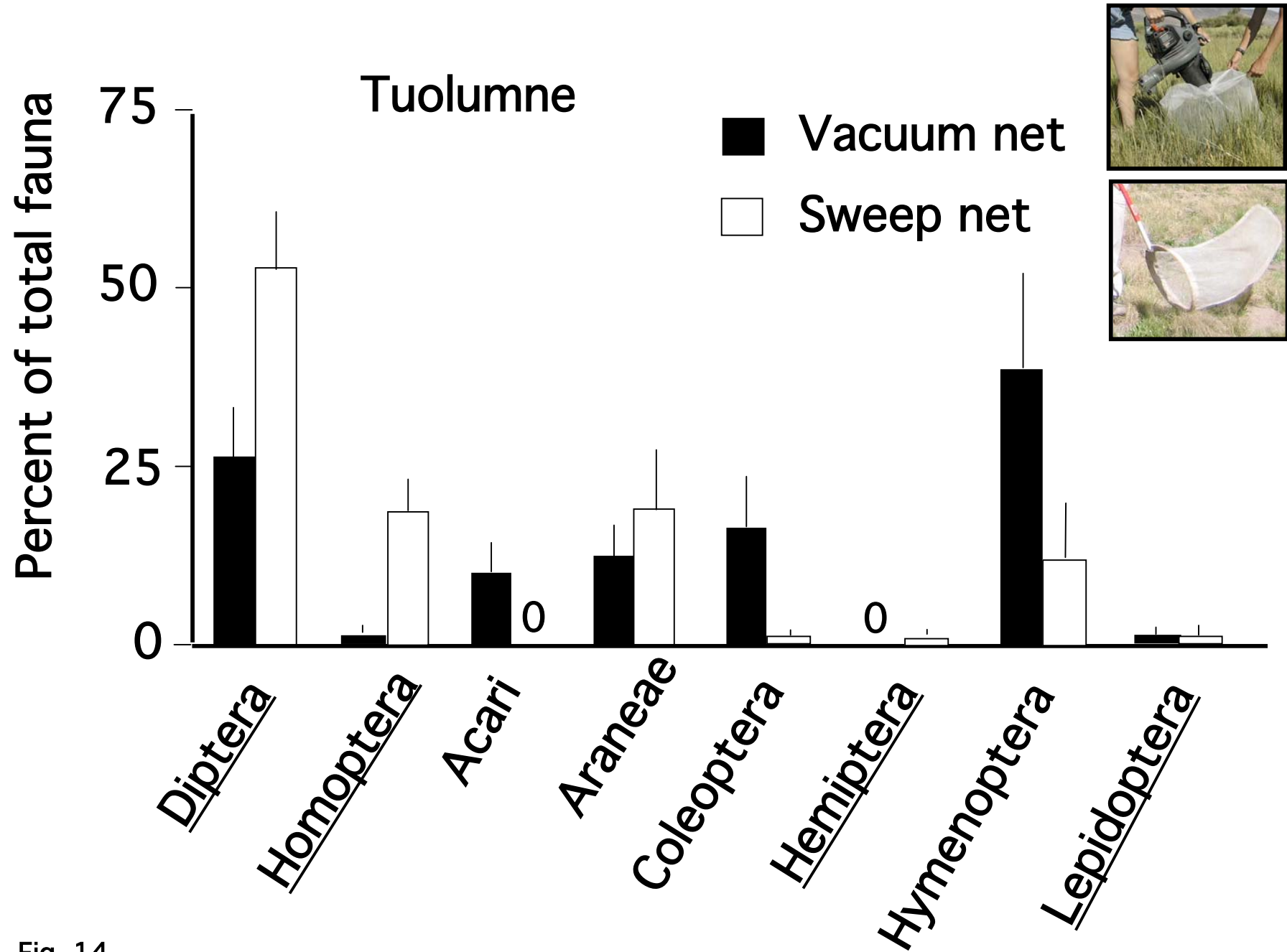


Fig. 14

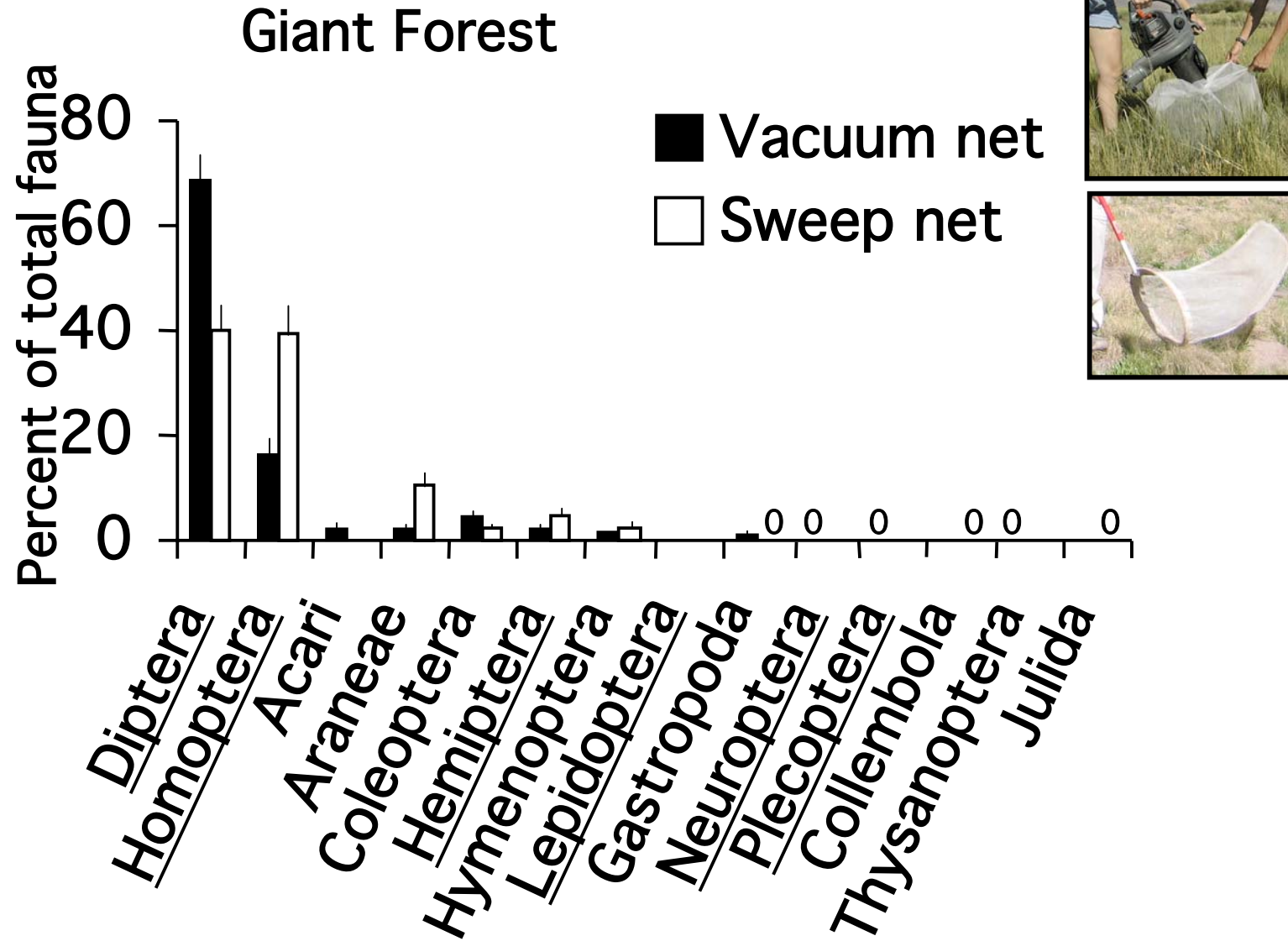


Fig. 15

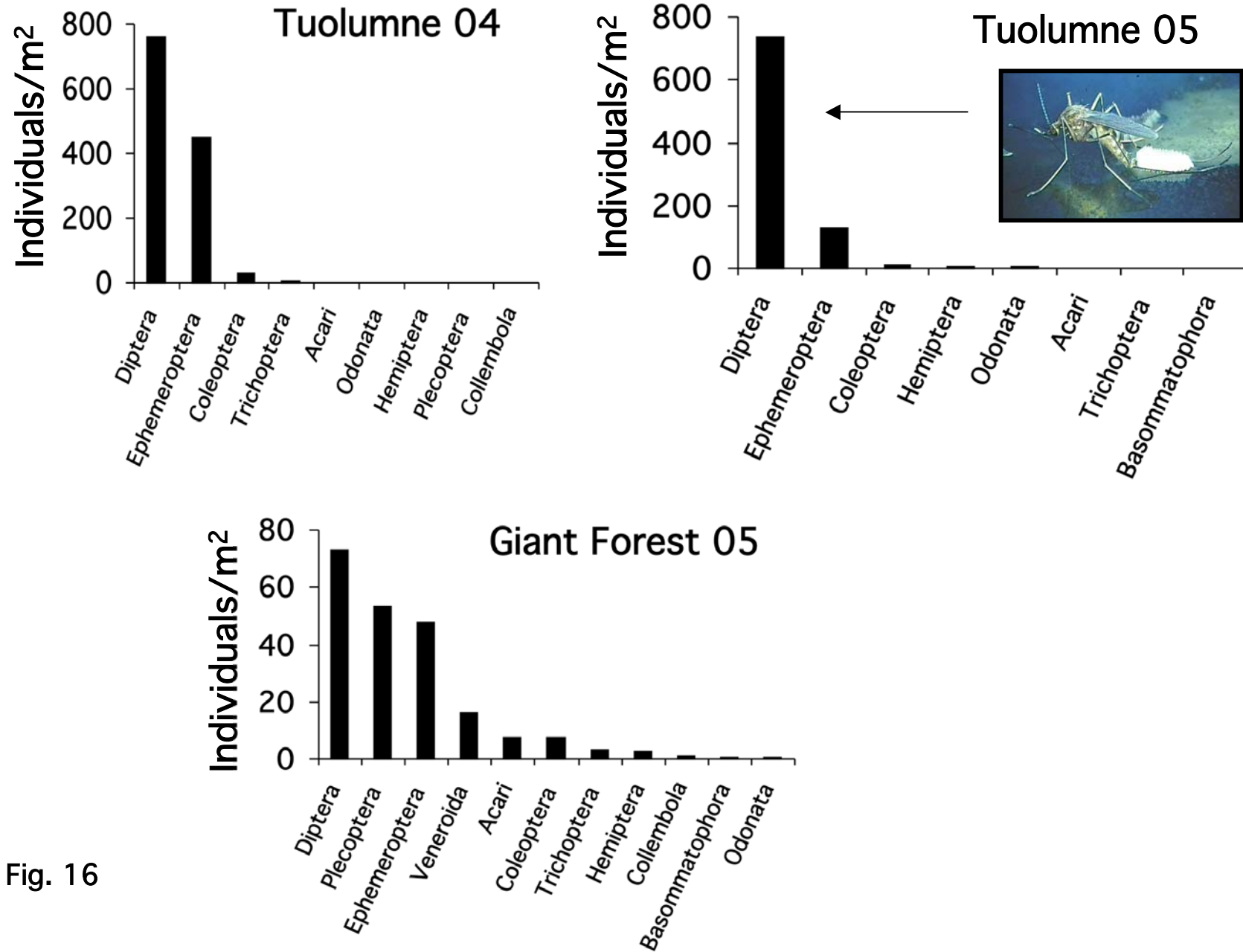


Fig. 16

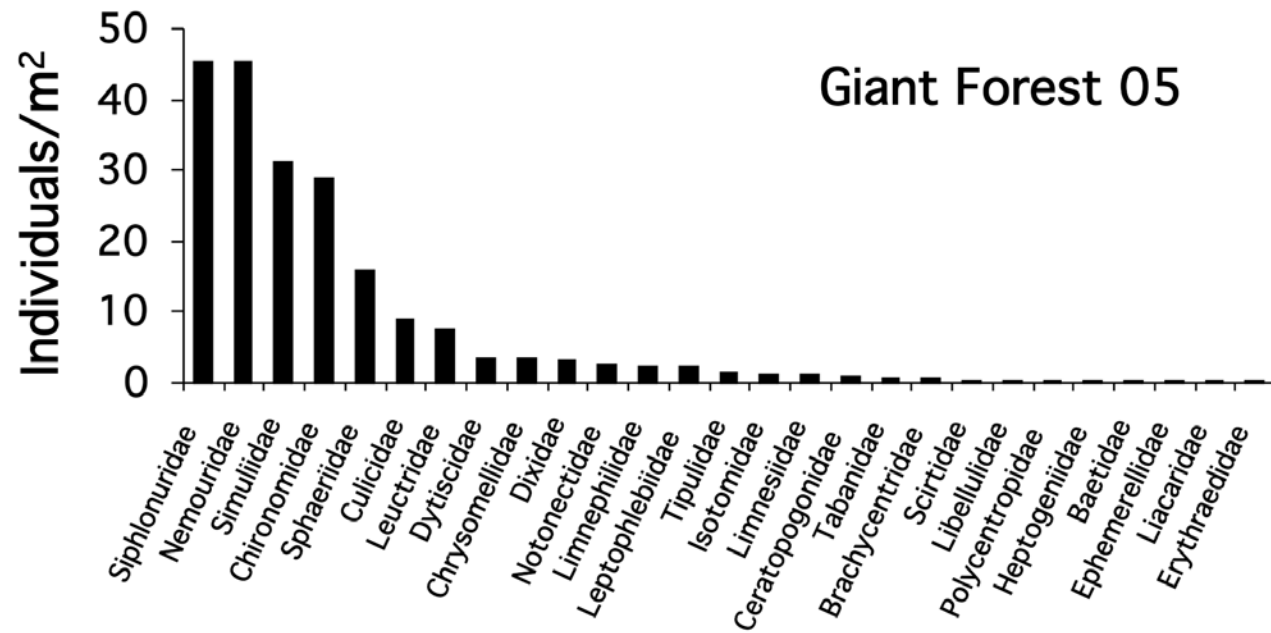
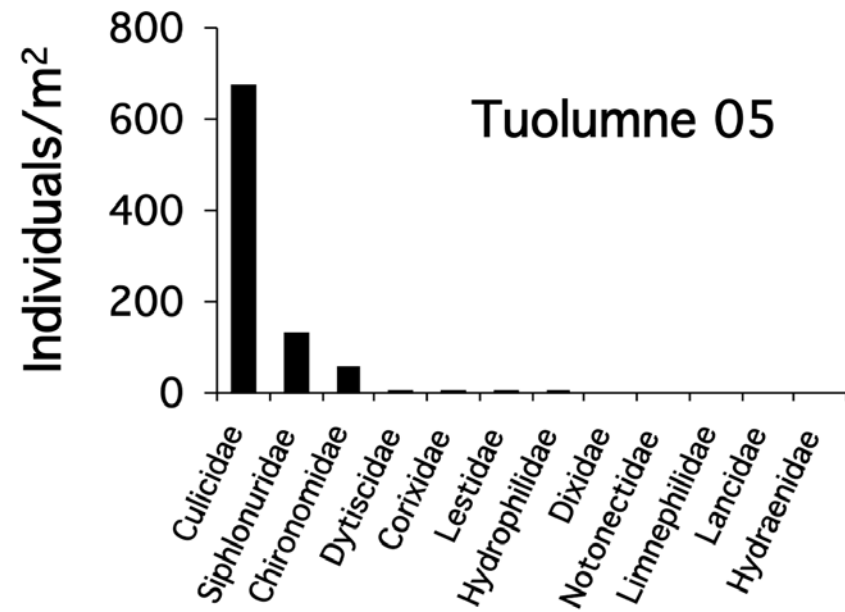
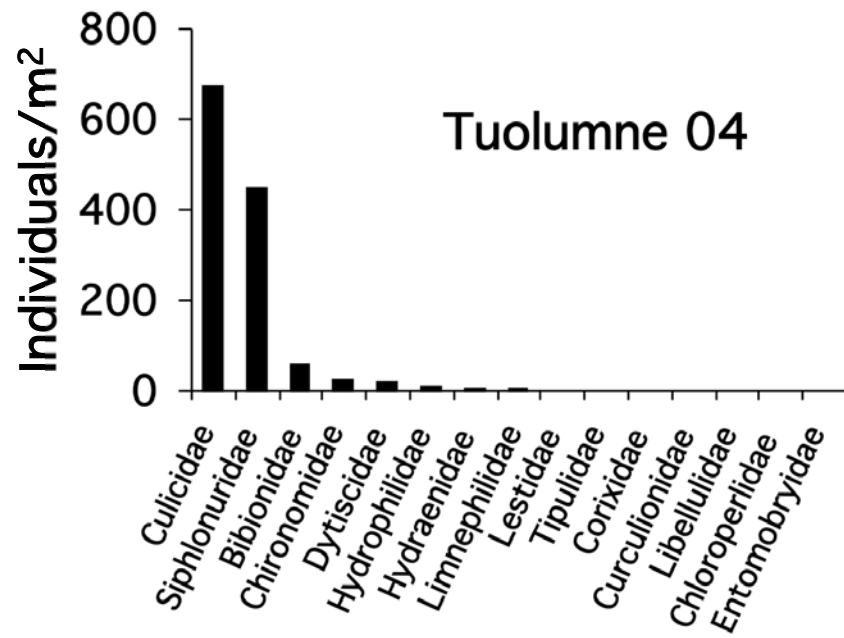


Fig. 17

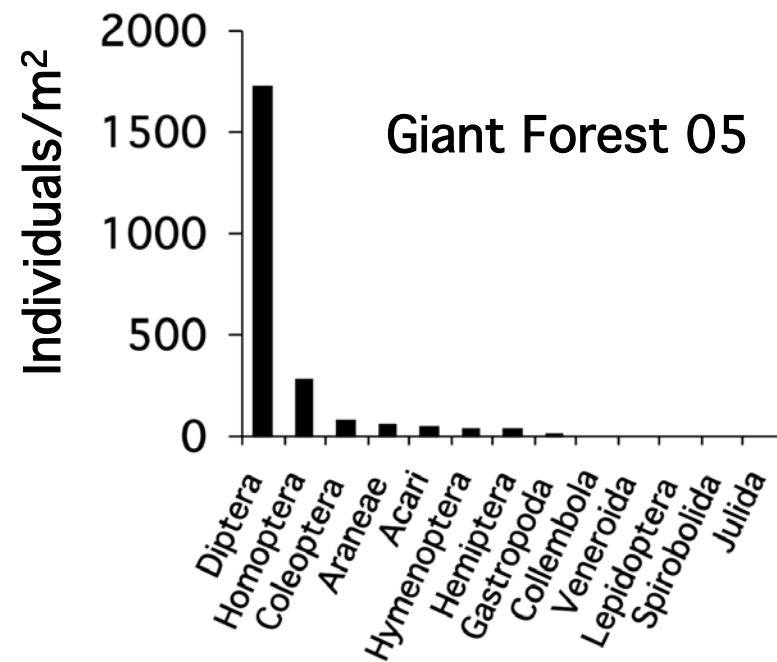
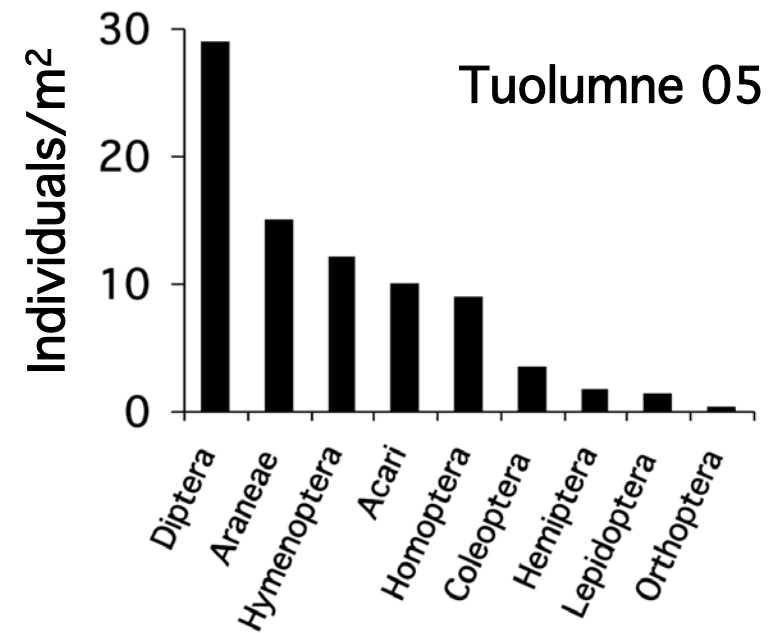
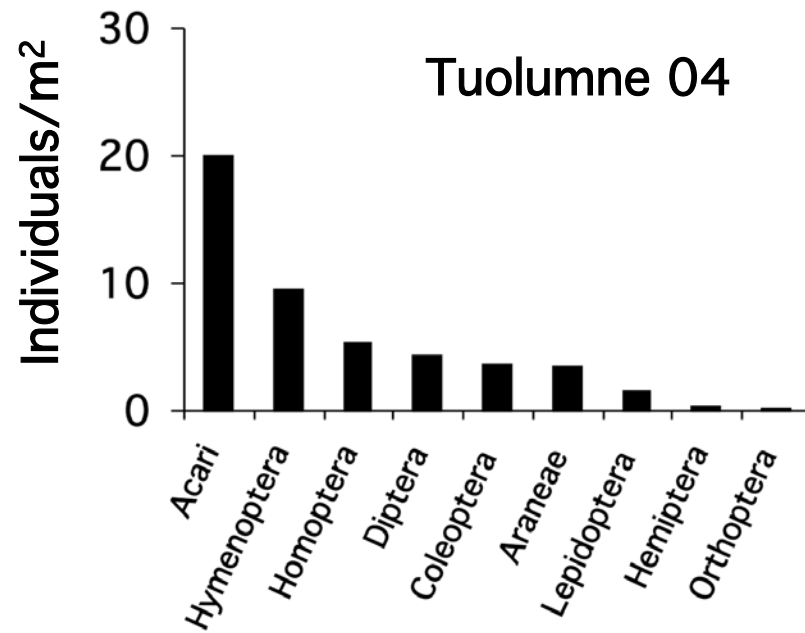


Fig. 18

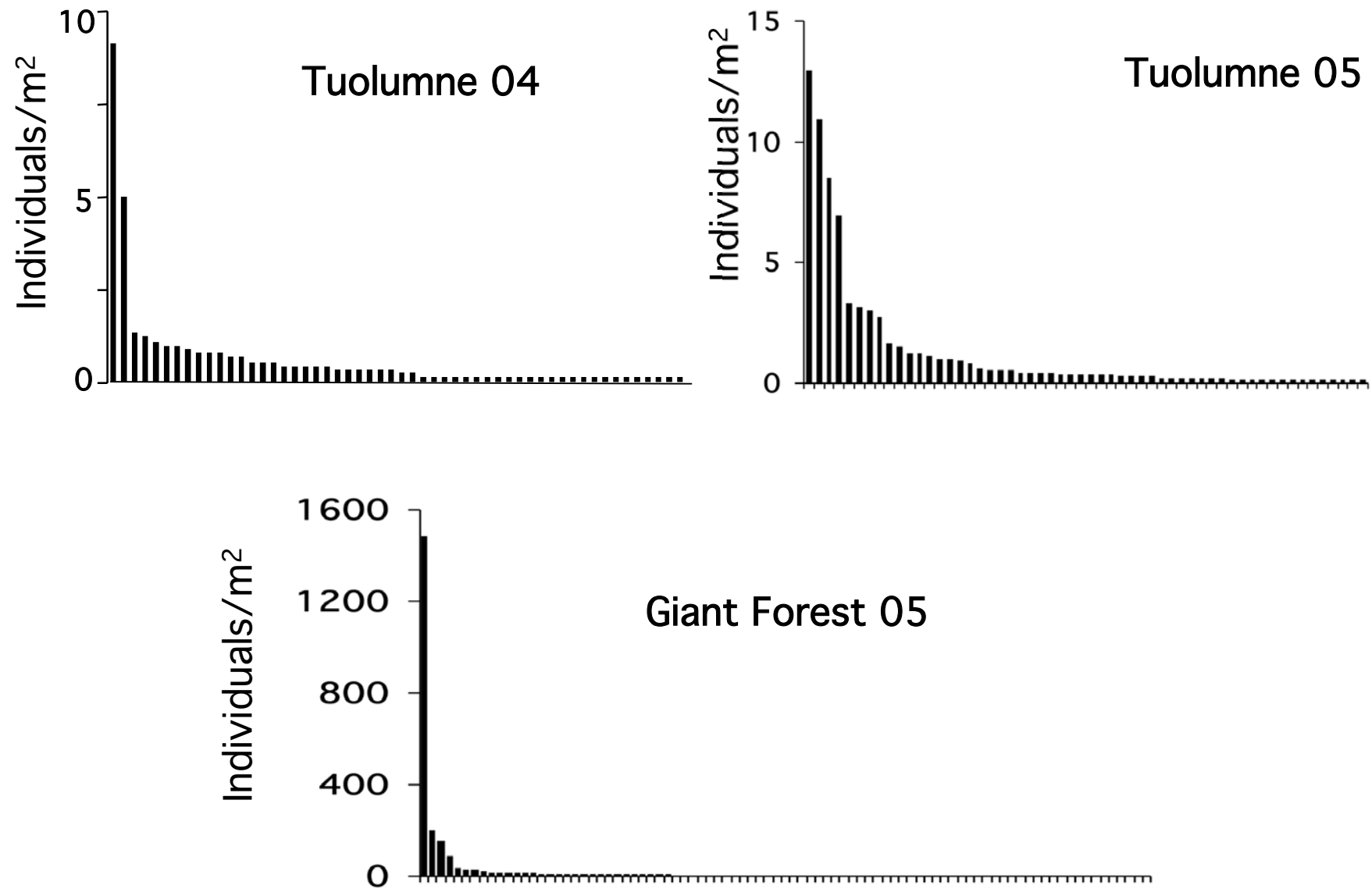


Fig. 19

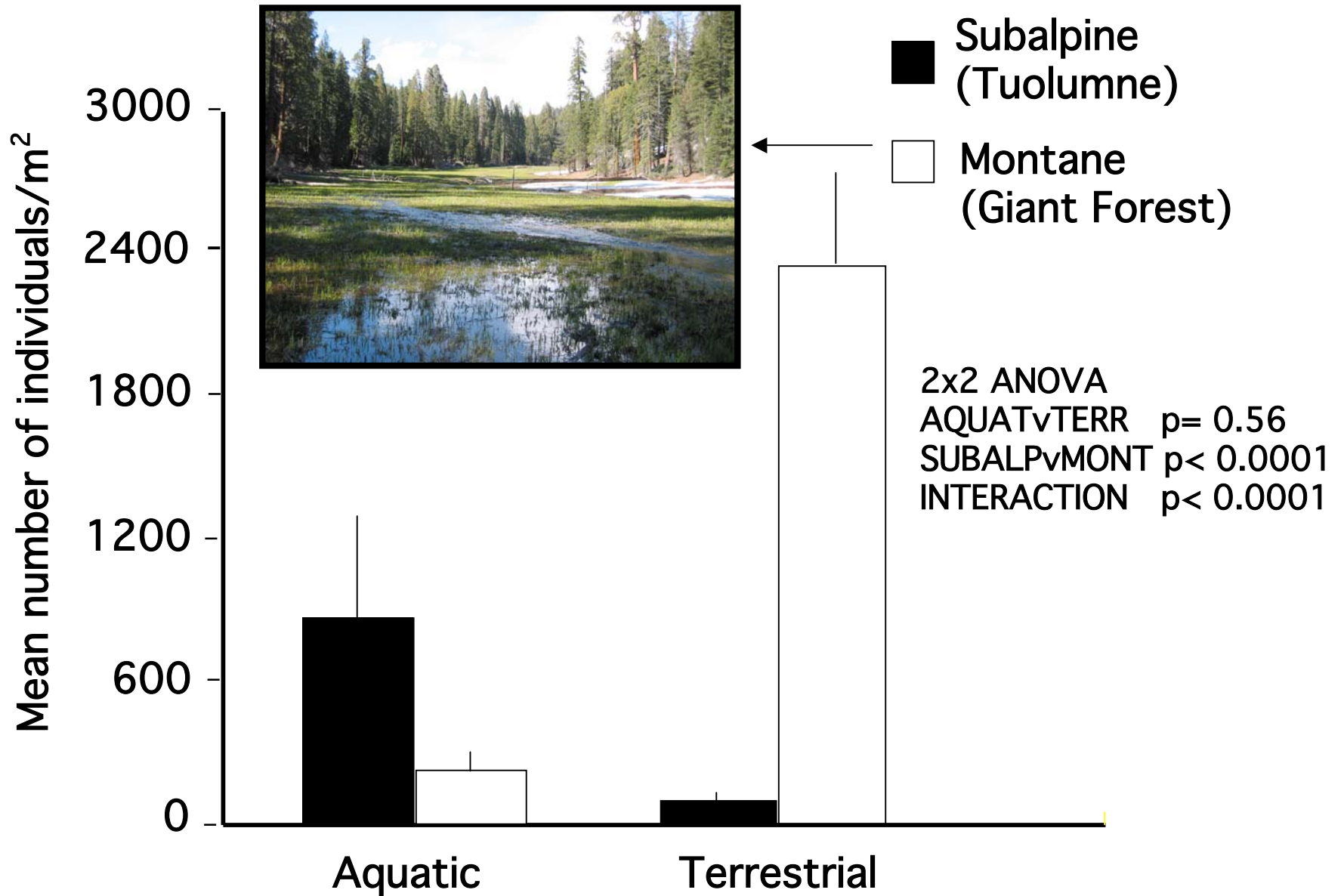


Fig. 20

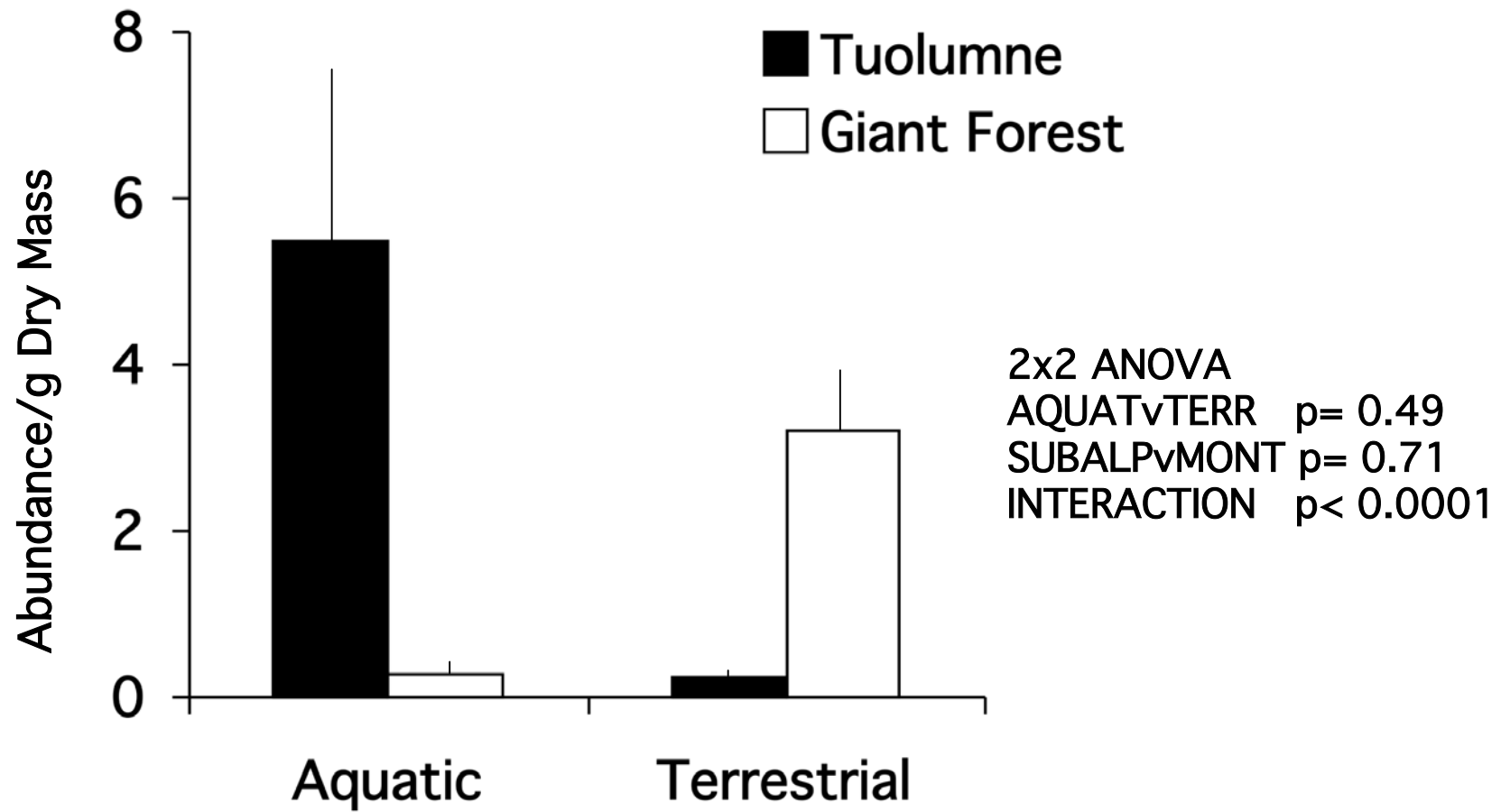


Fig. 21

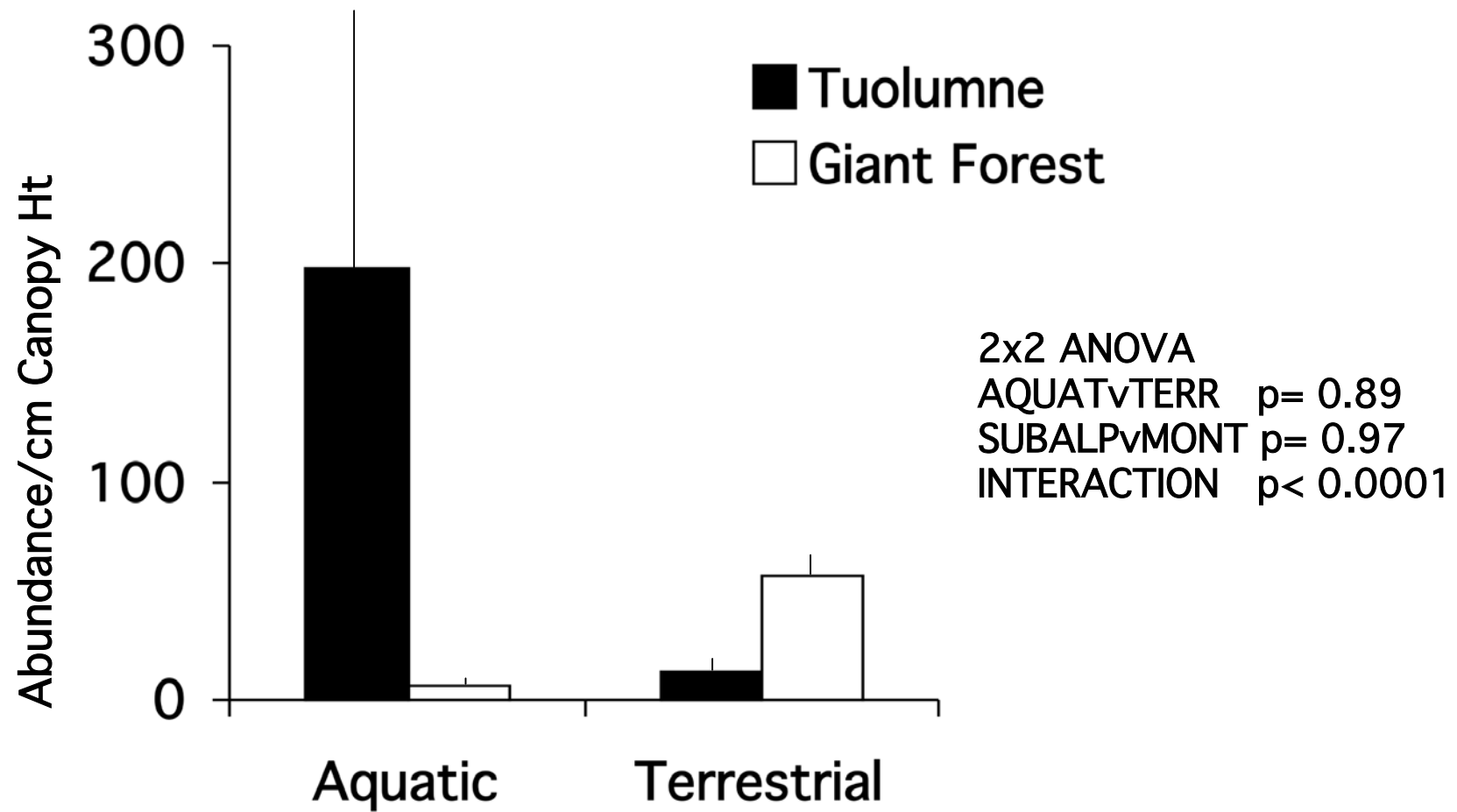


Fig. 22

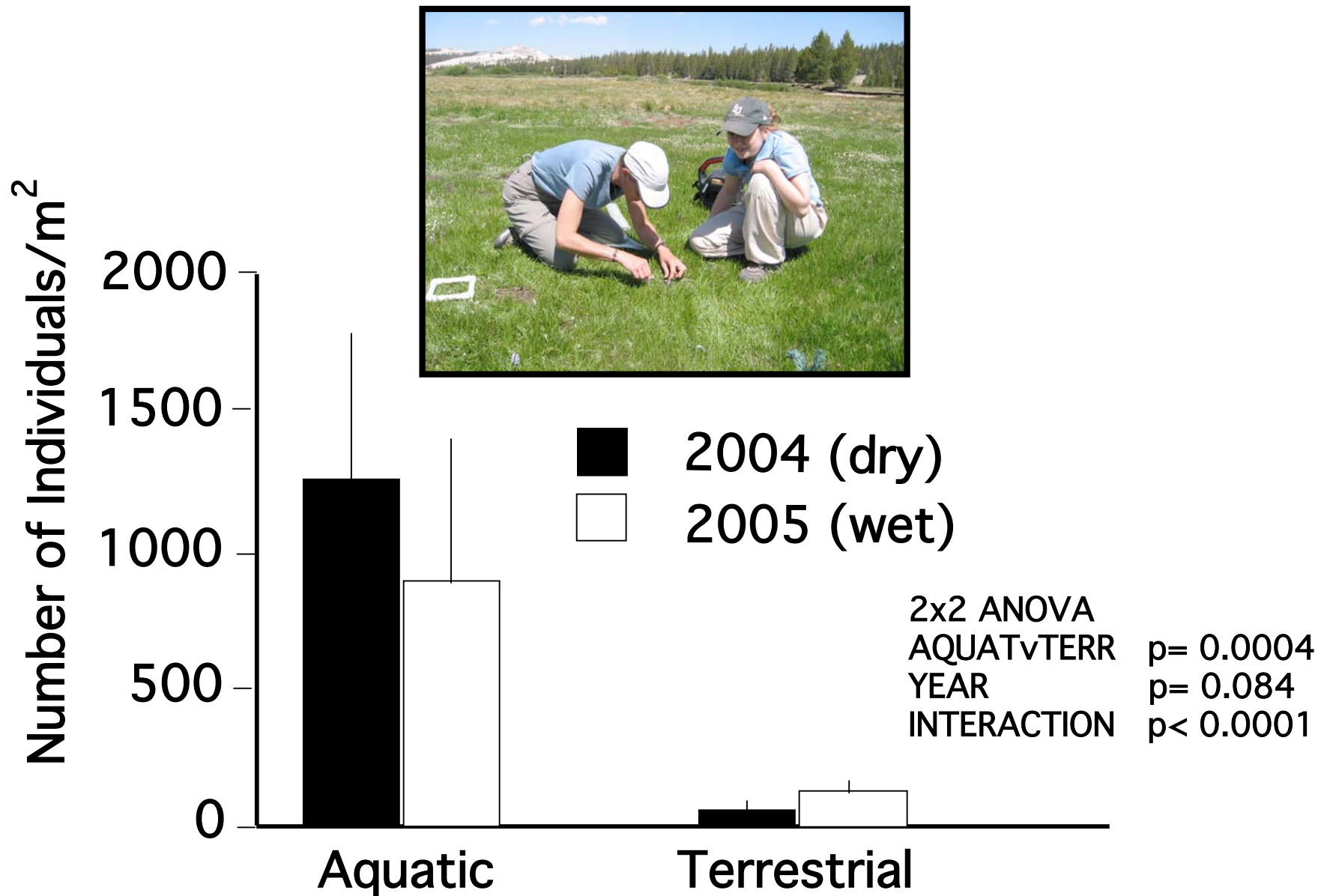


Fig. 23

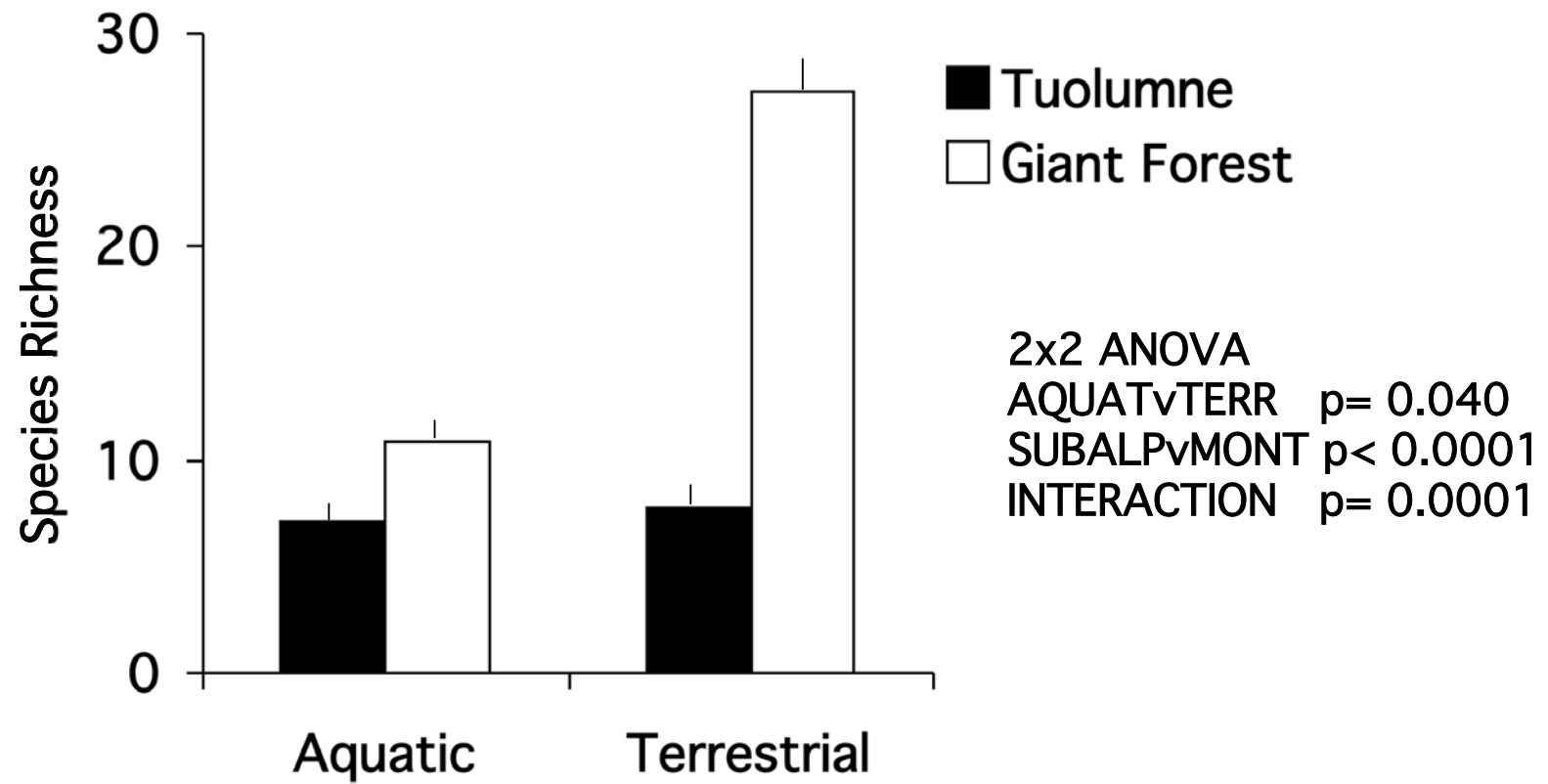


Fig. 24

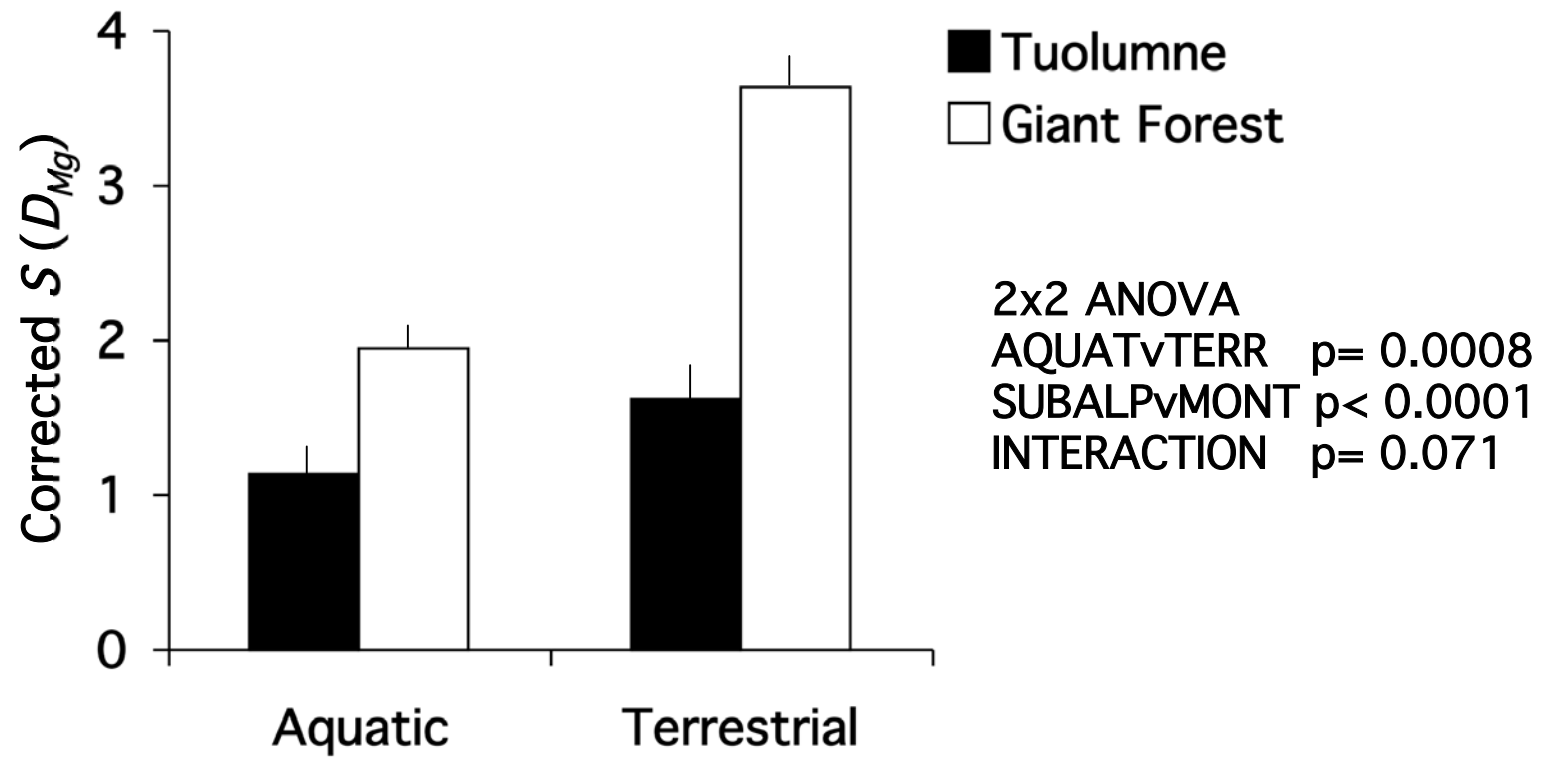


Fig. 25

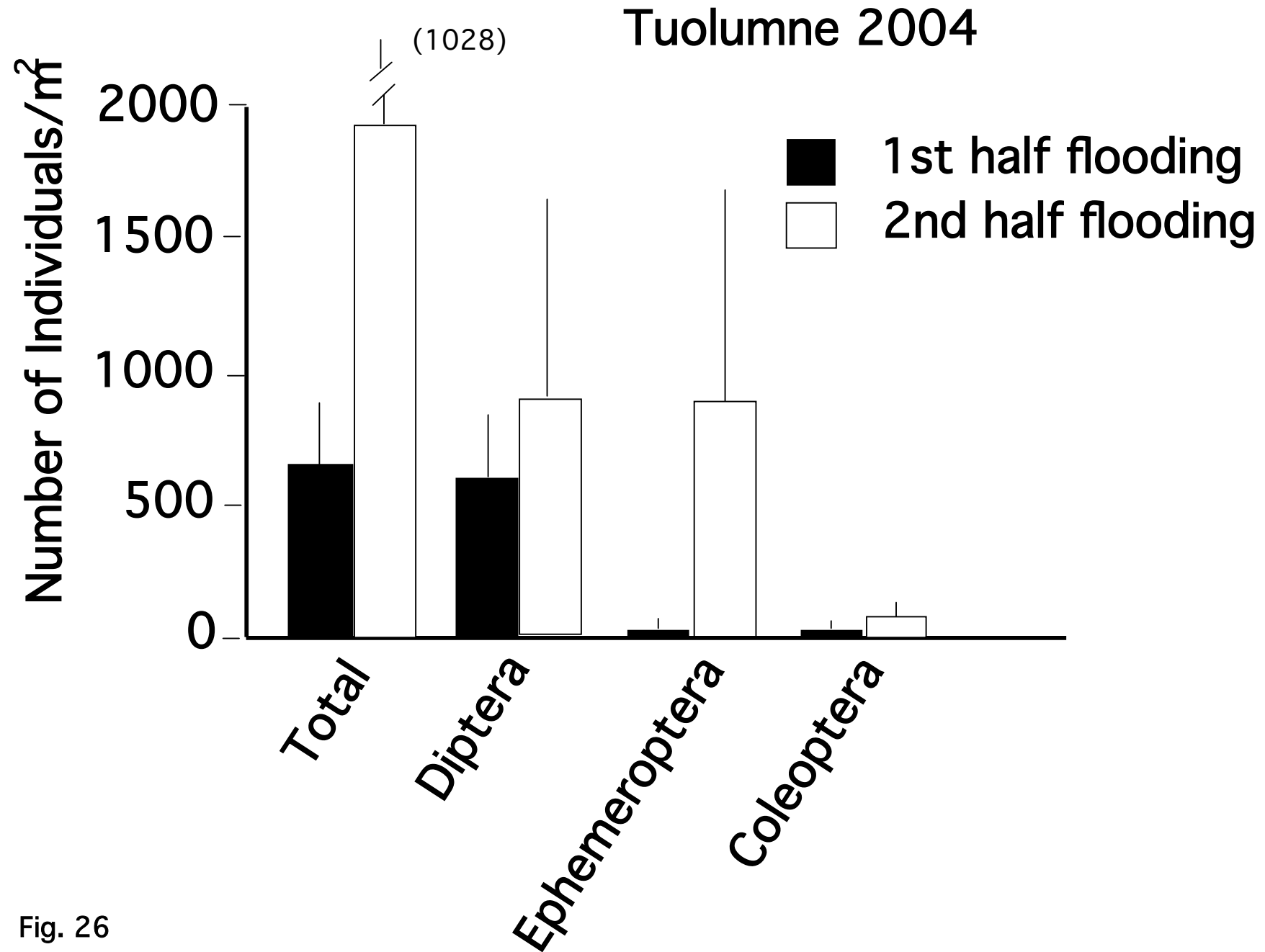


Fig. 26

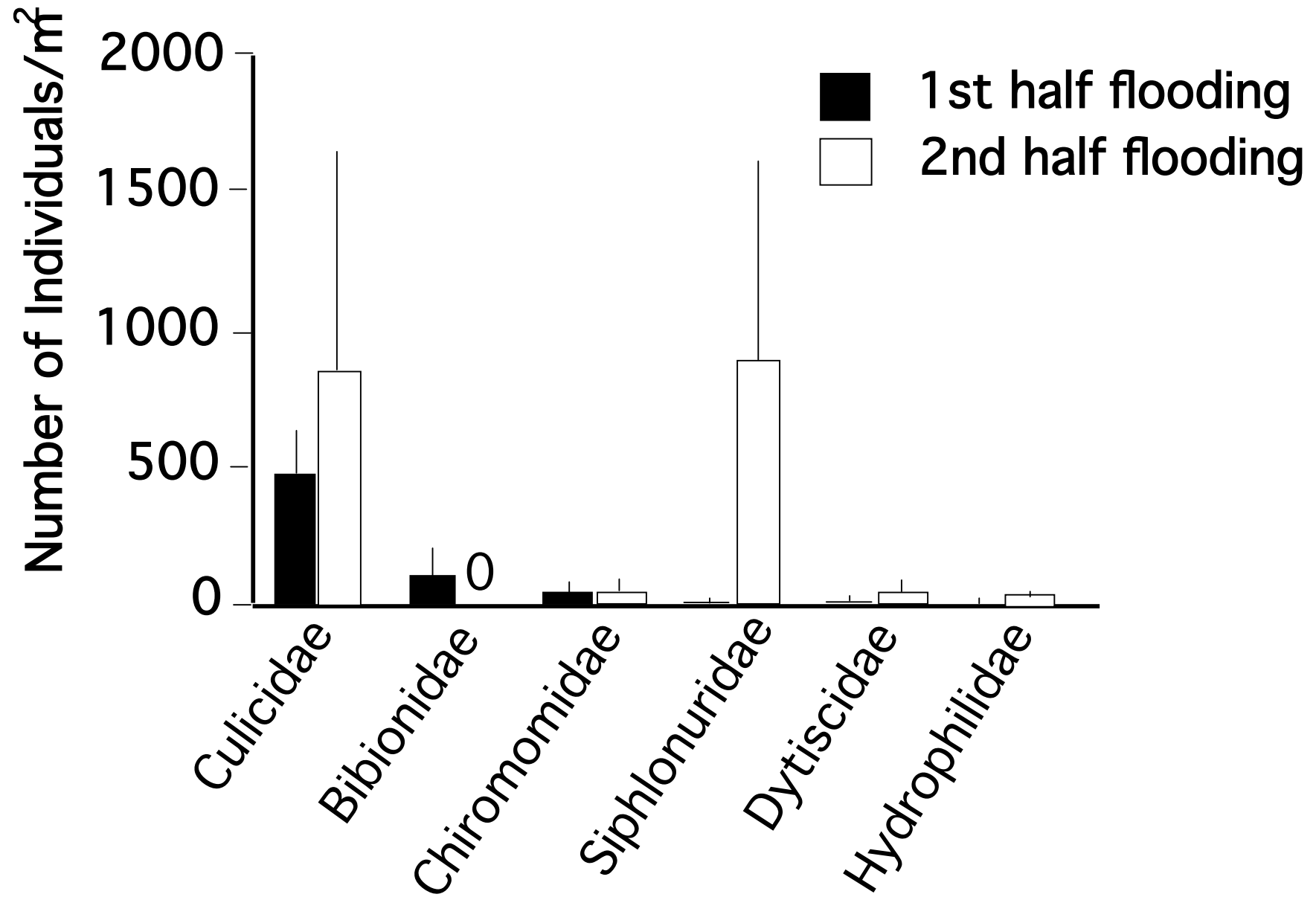


Fig. 27

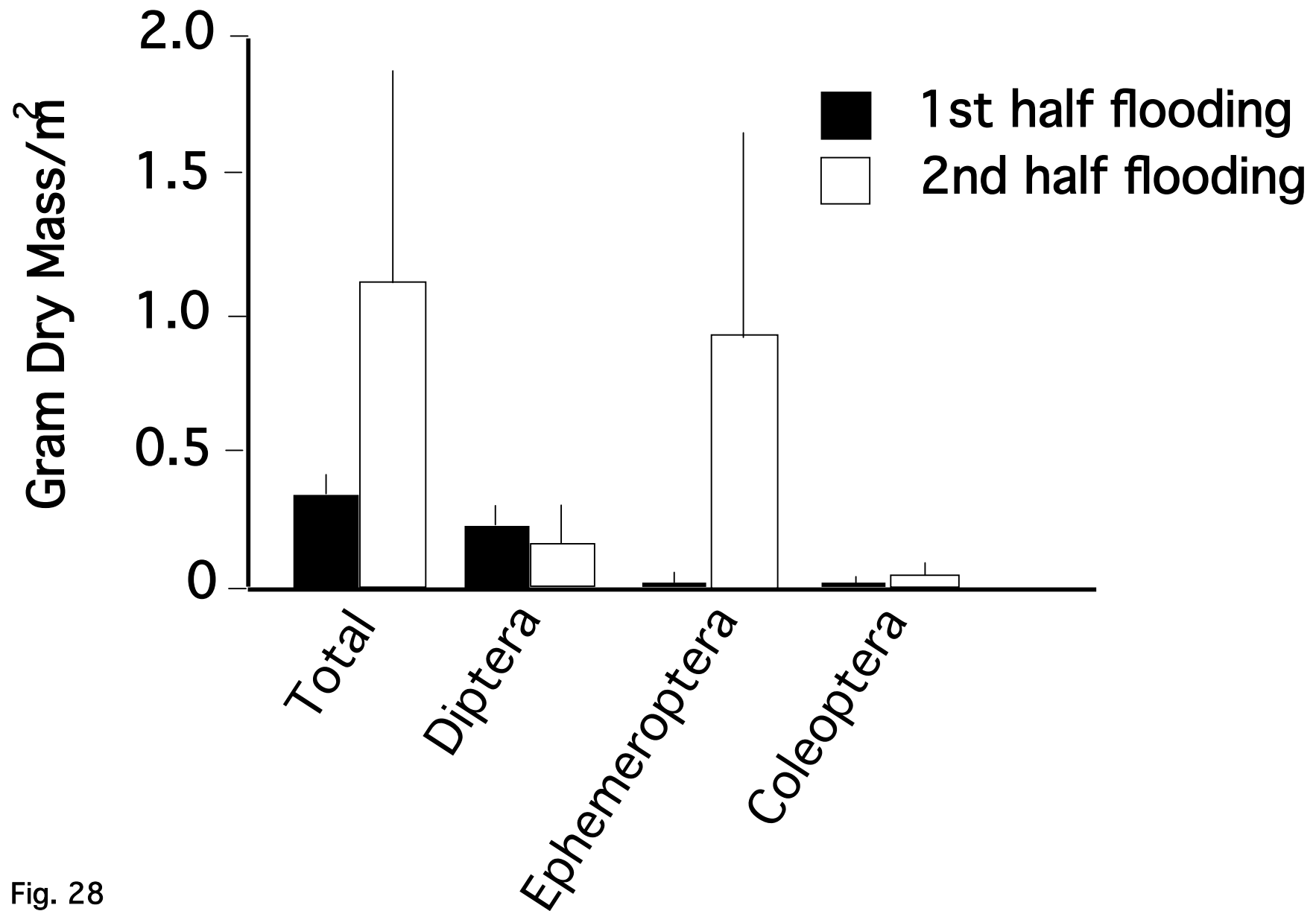


Fig. 28

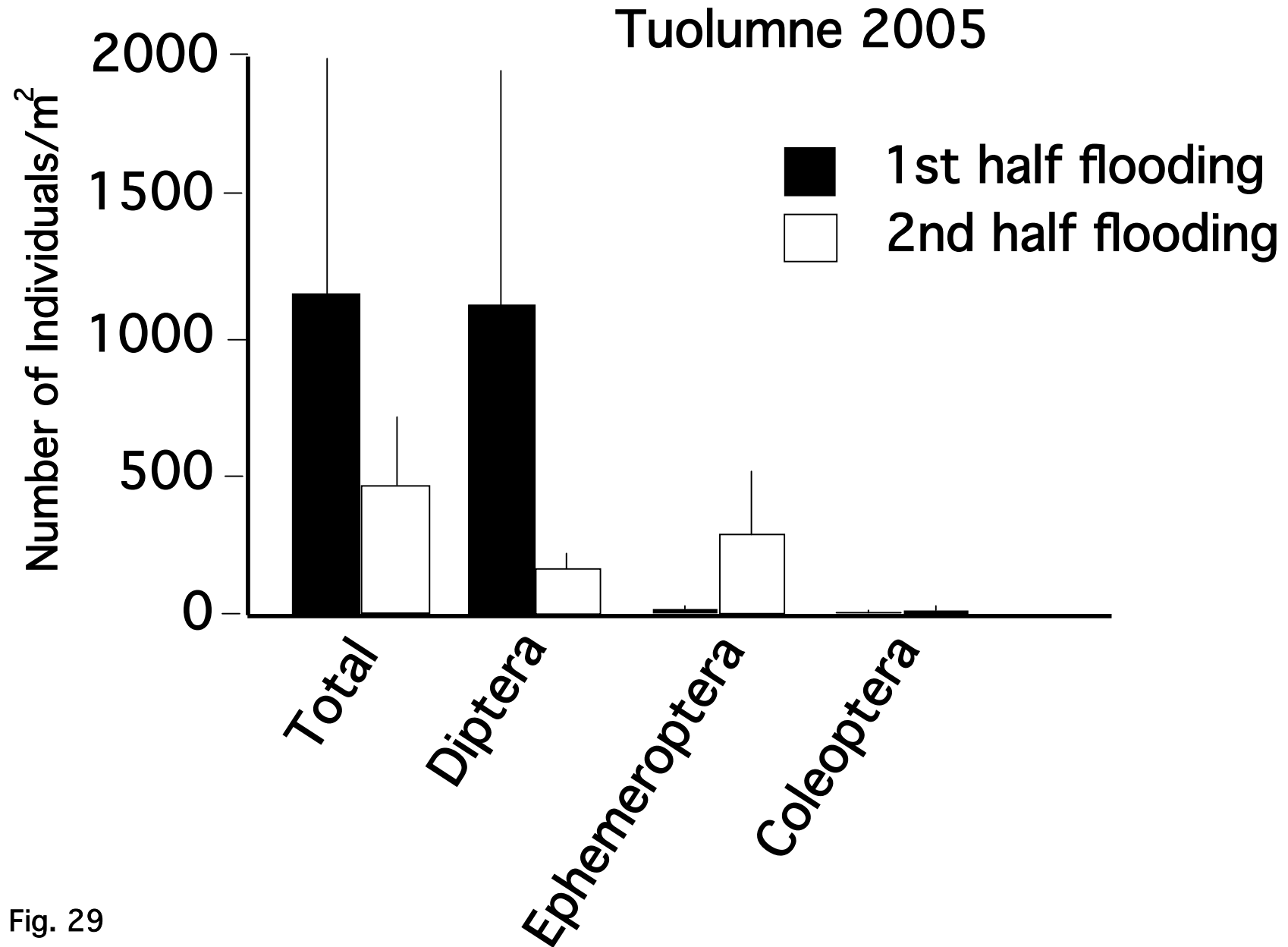


Fig. 29

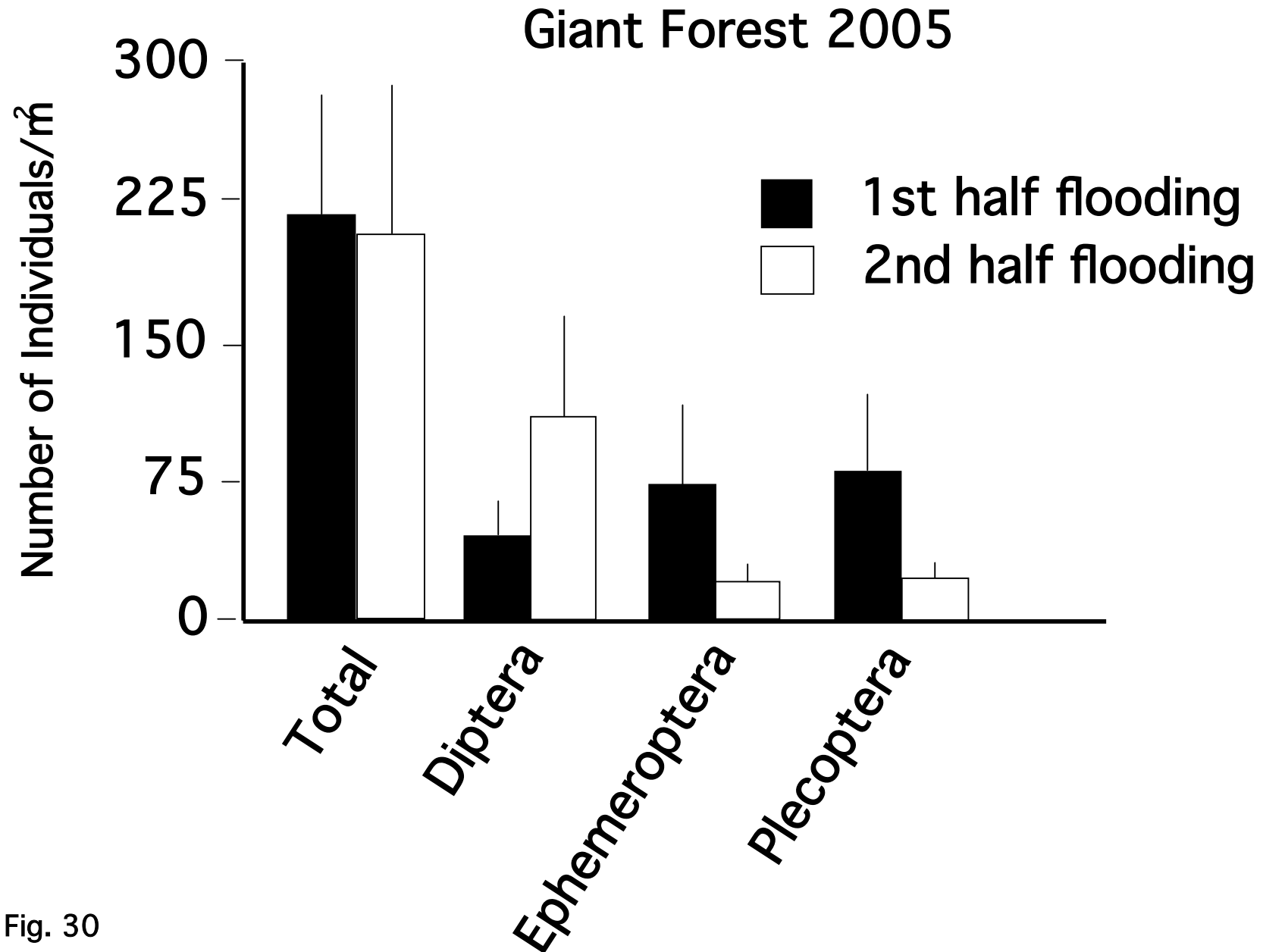


Fig. 30

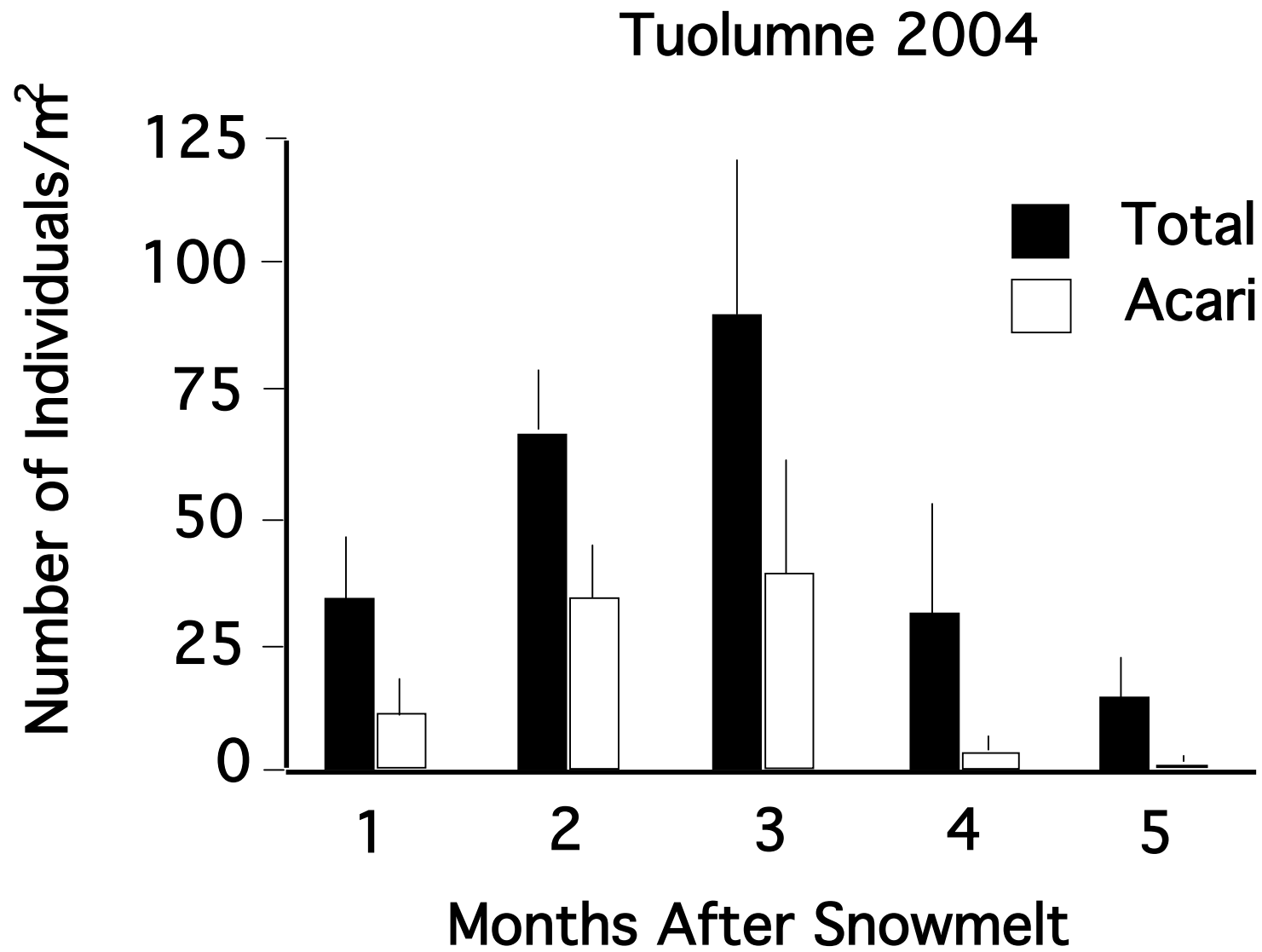


Fig. 31

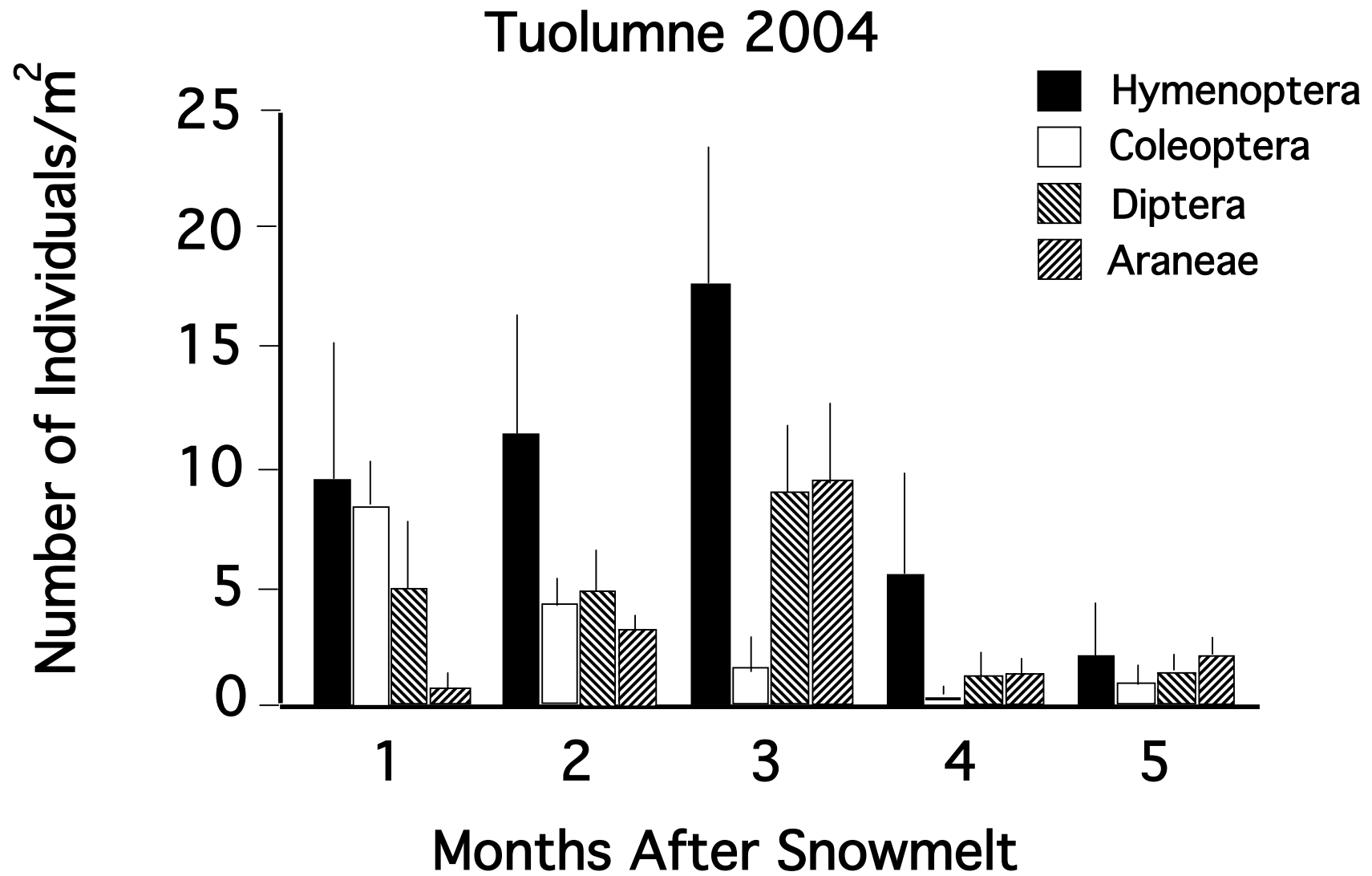


Fig. 32

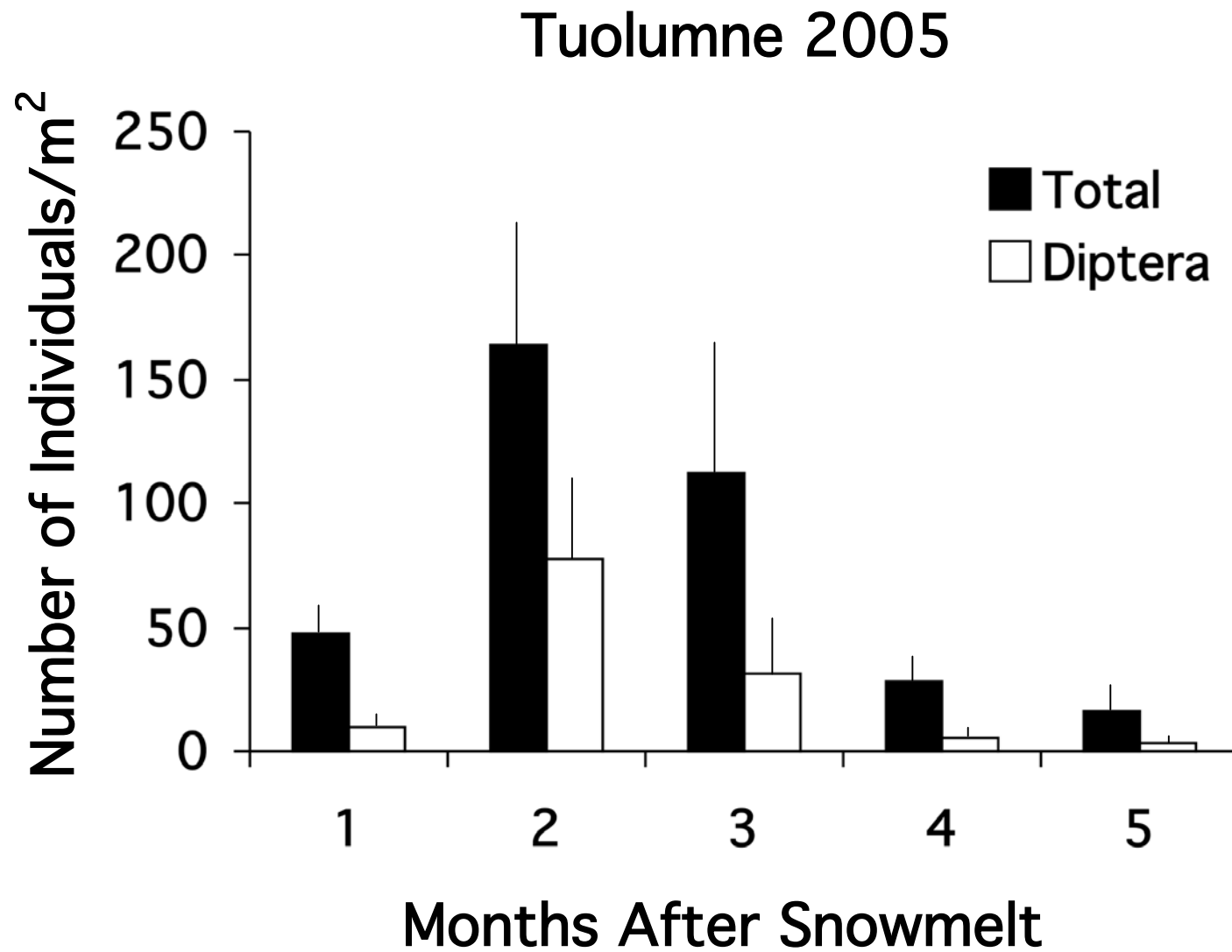


Fig. 33

Tuolumne 2005

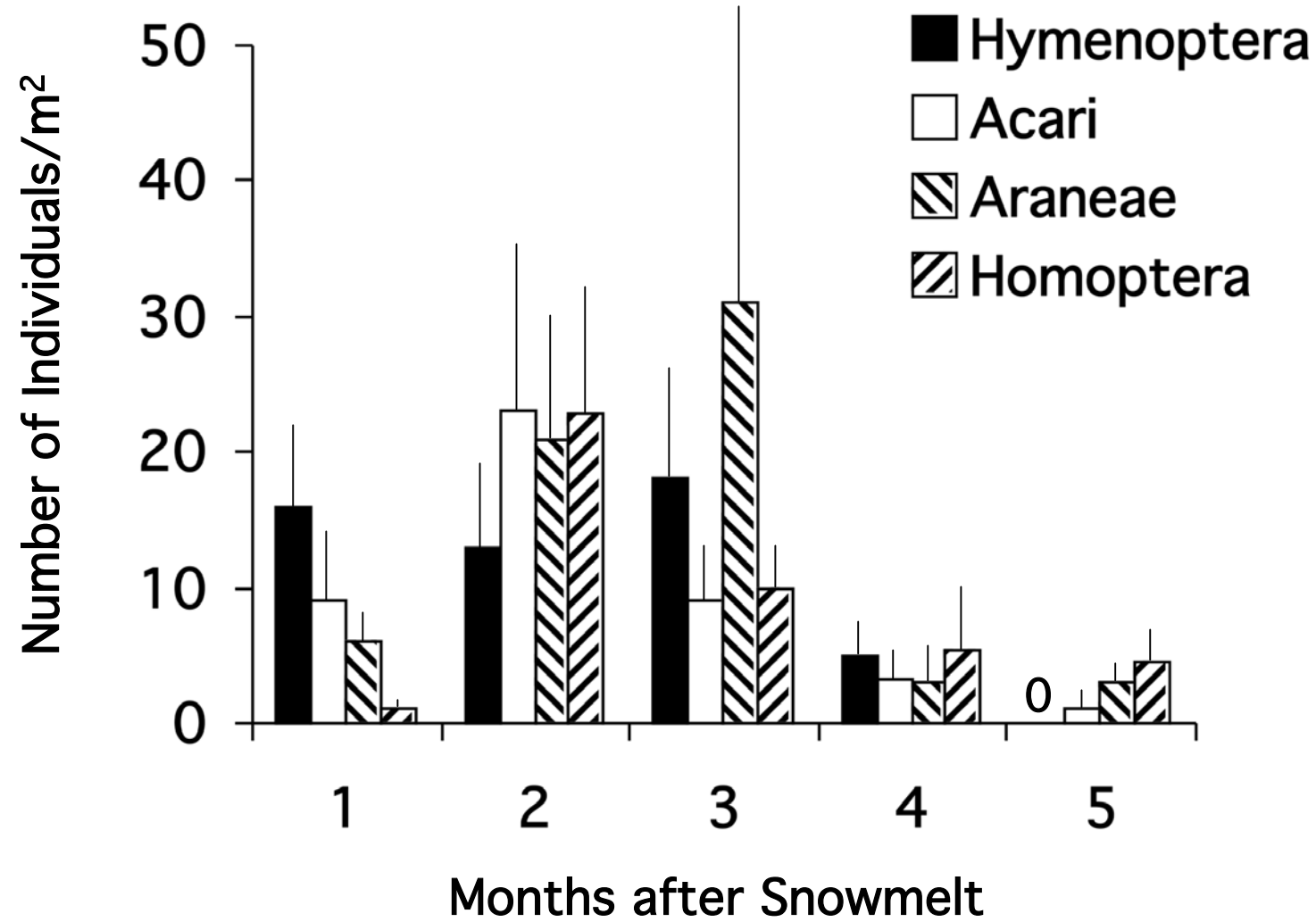


Fig. 34

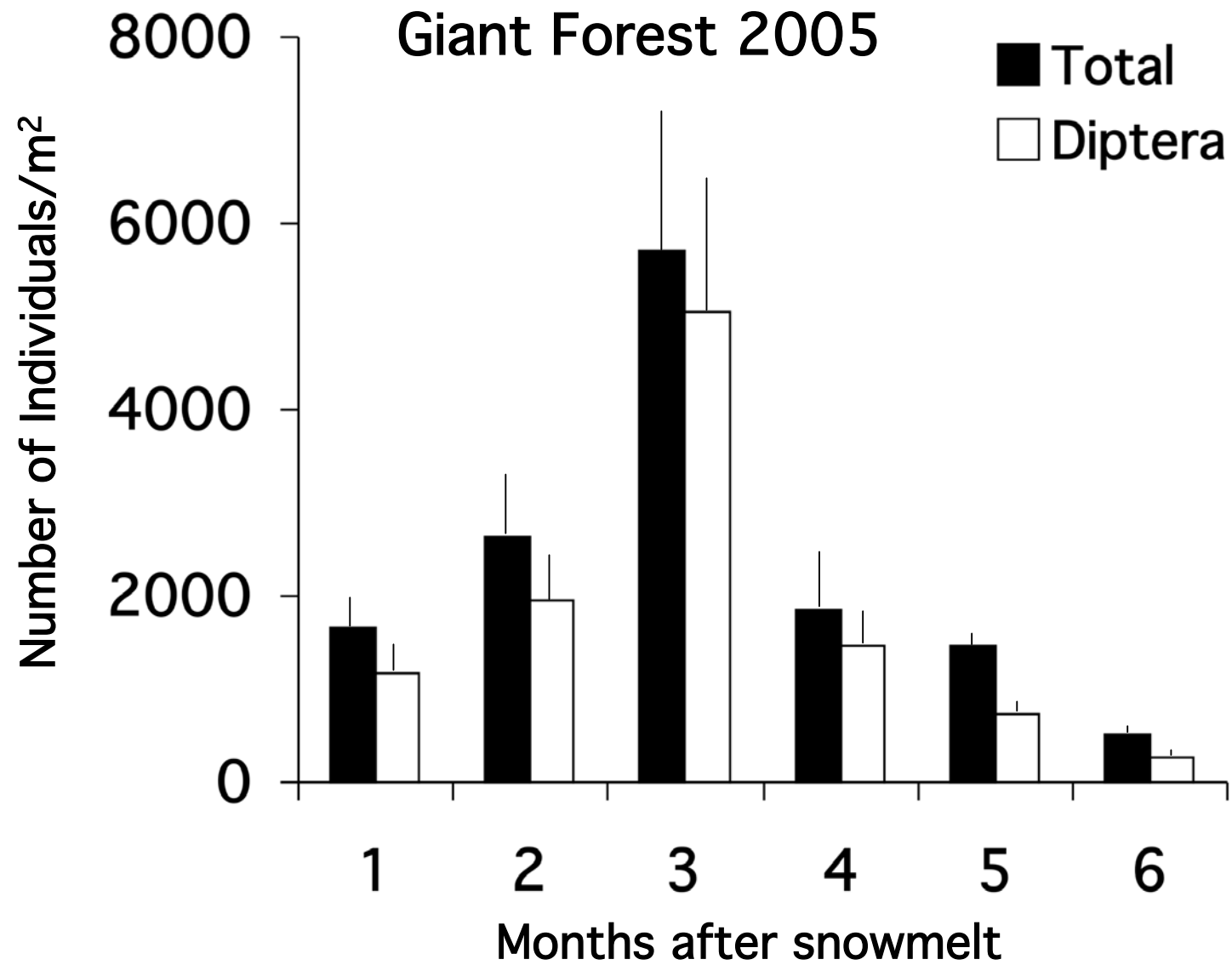


Fig. 35

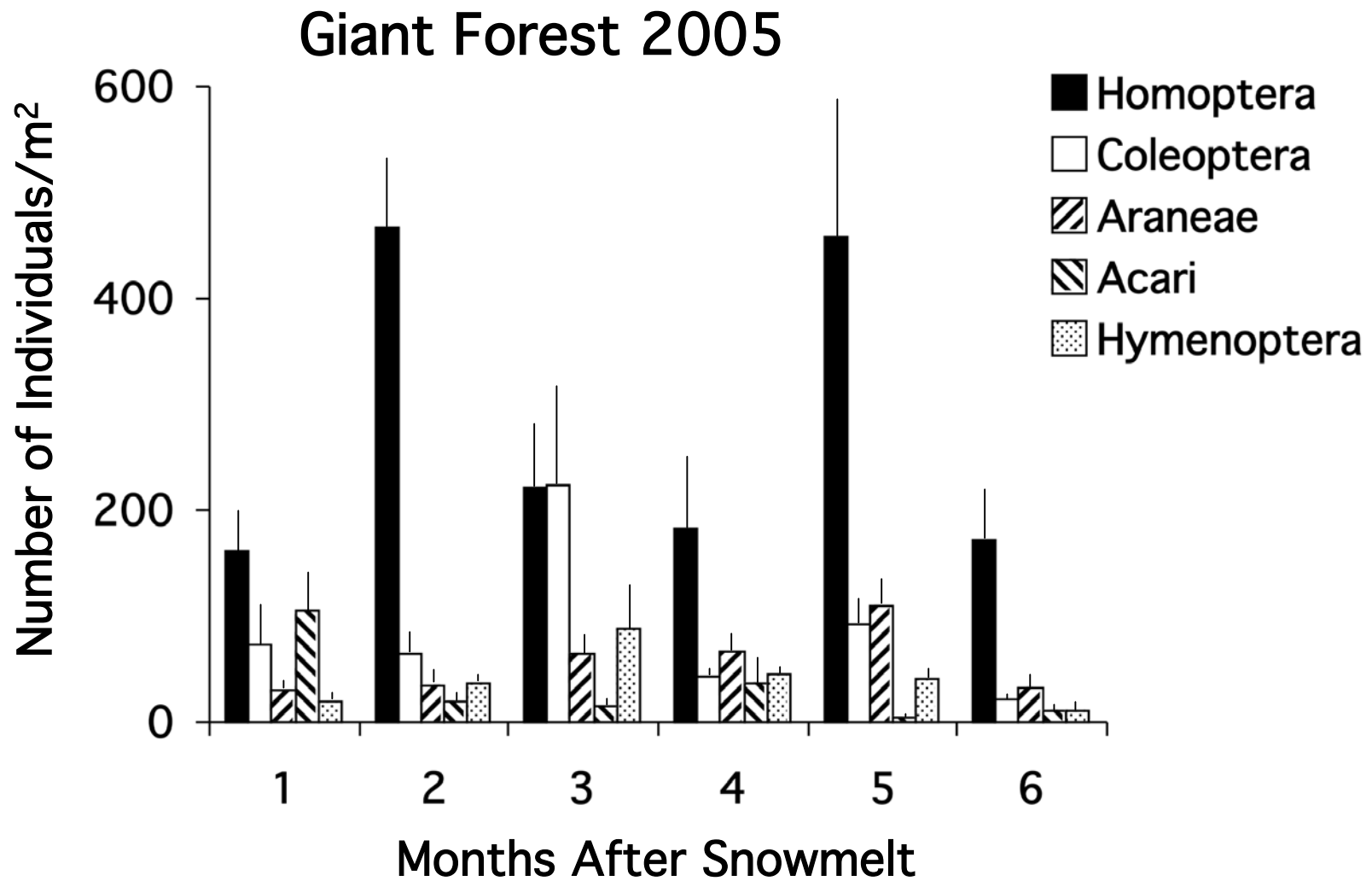


Fig. 36

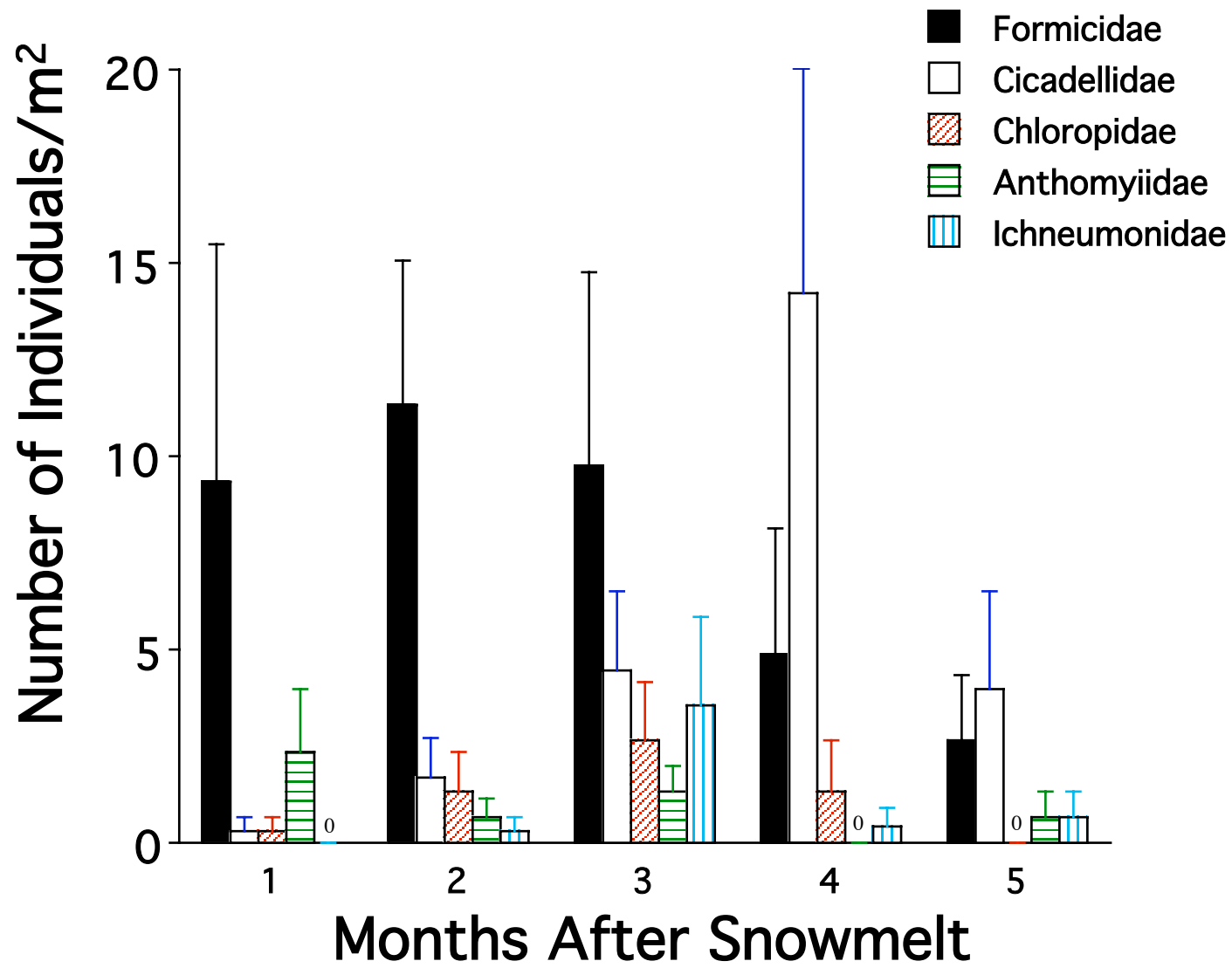


Fig. 37

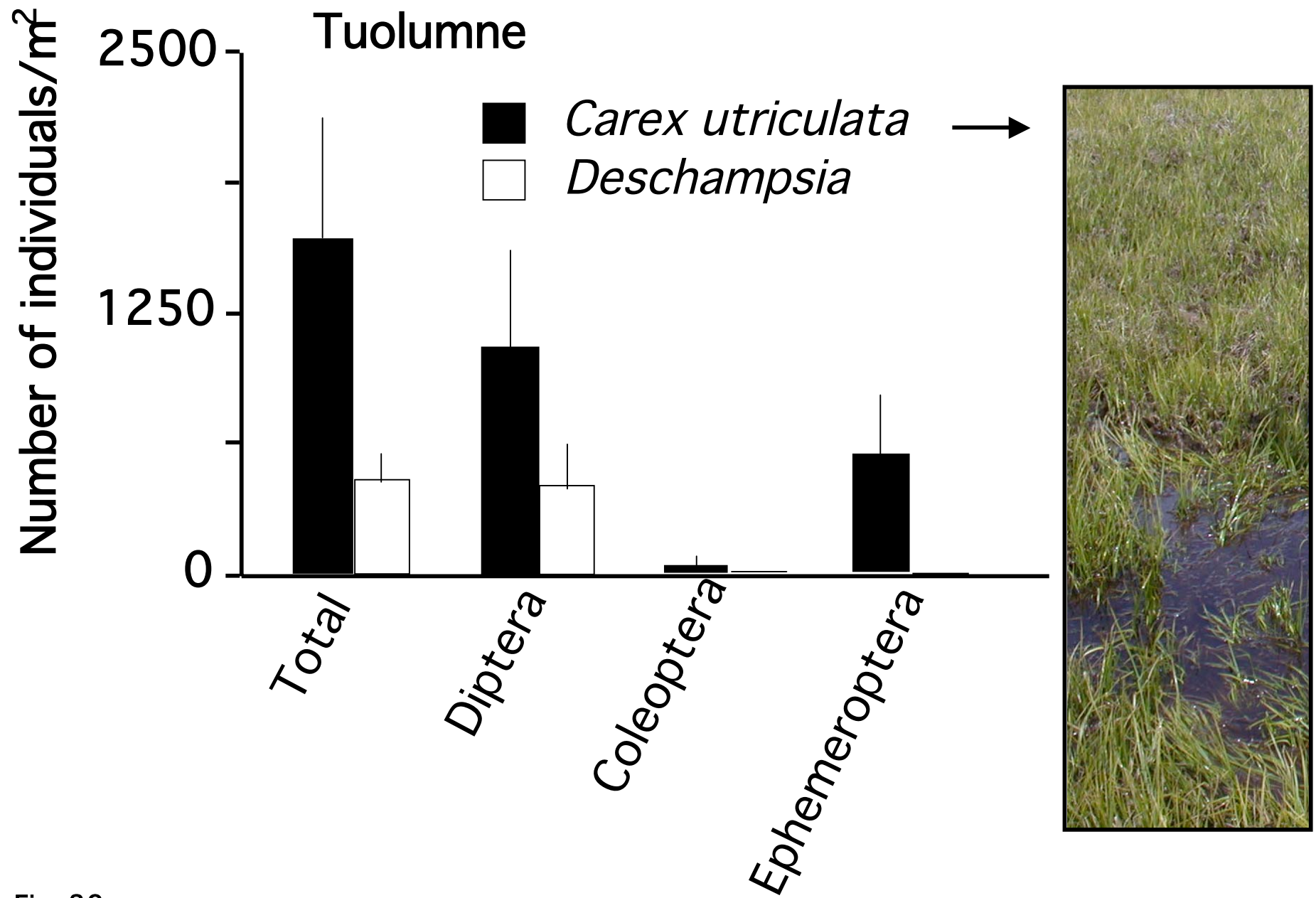


Fig. 38

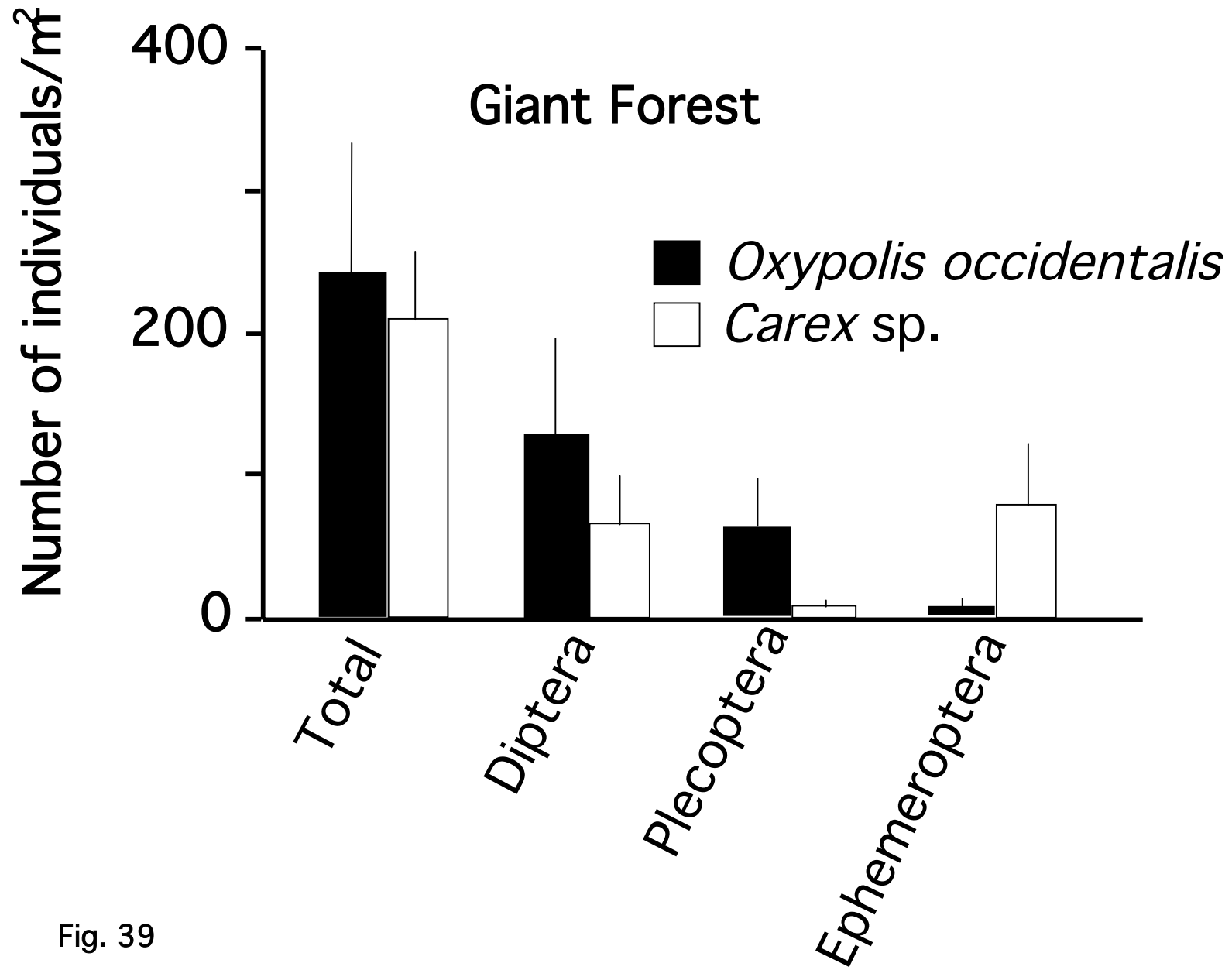


Fig. 39

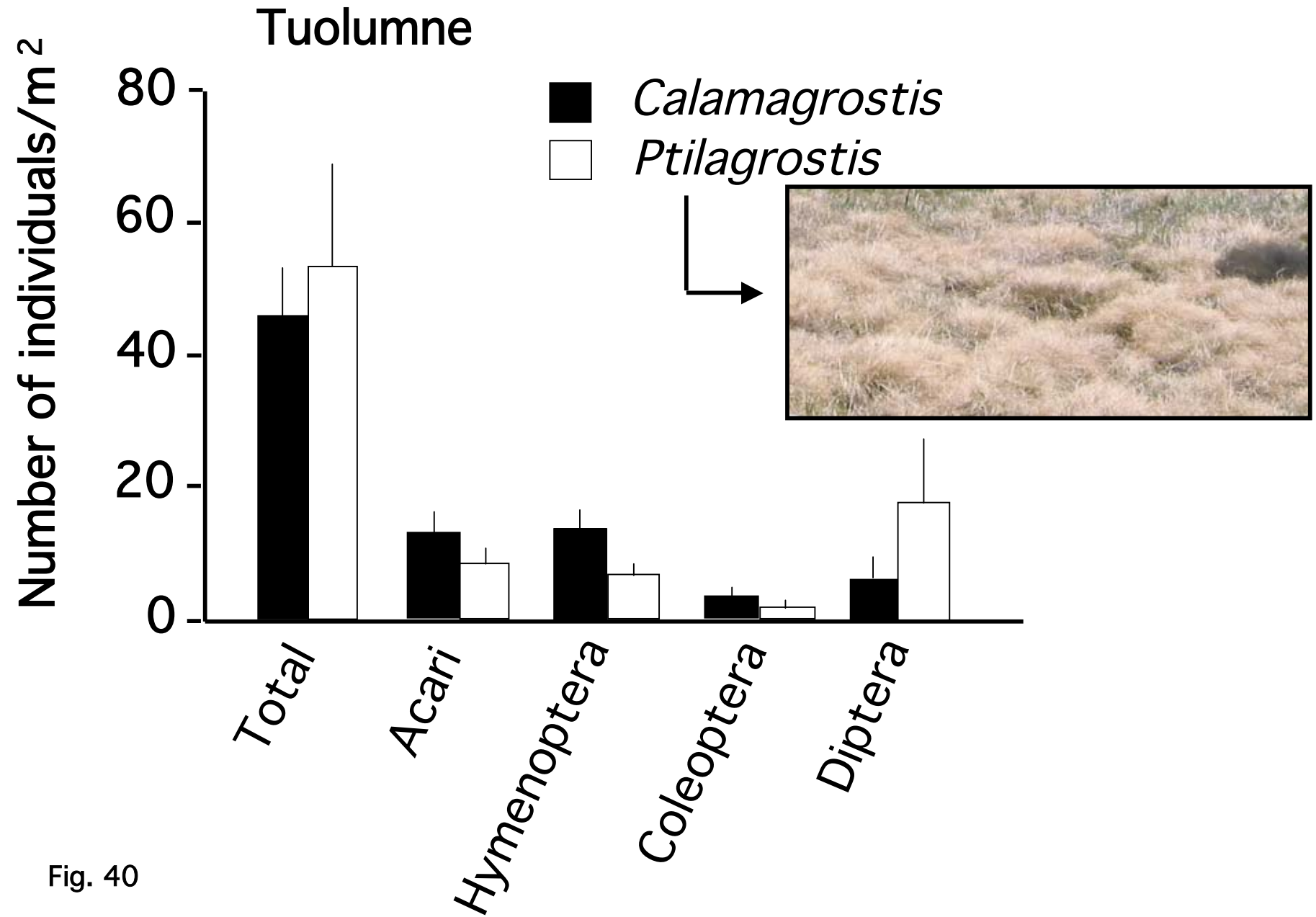


Fig. 40

Giant Forest

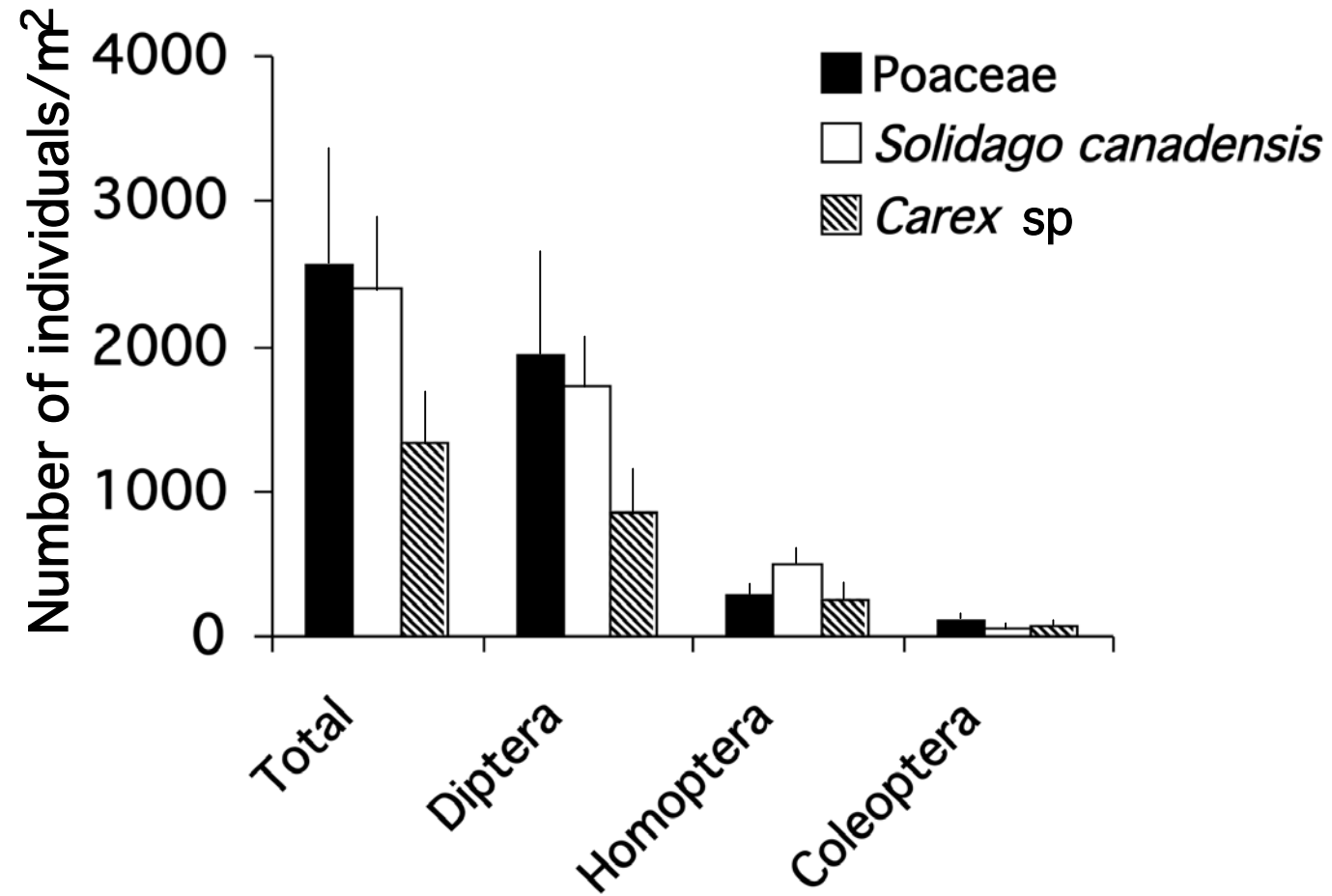


Fig. 41

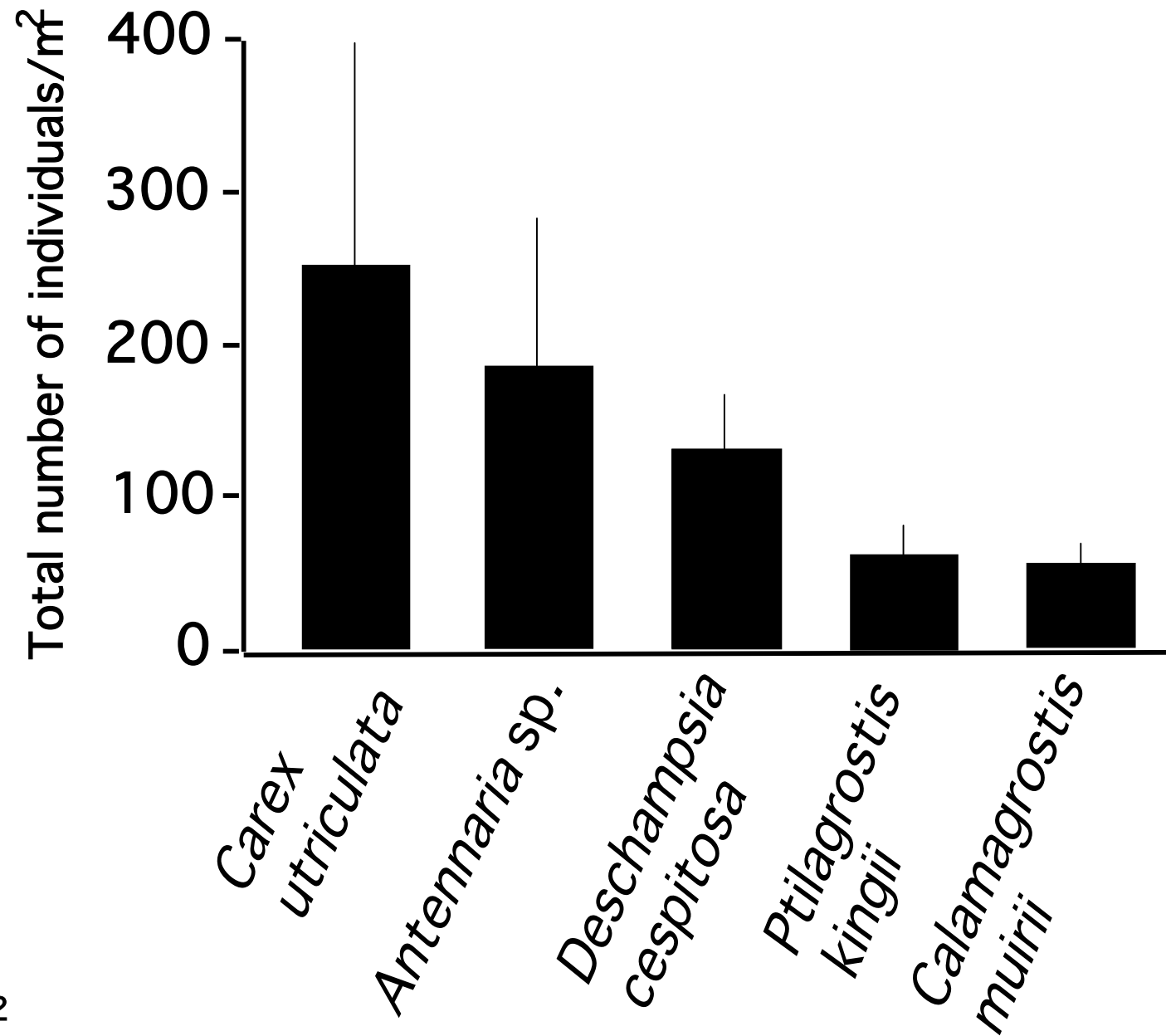


Fig. 42

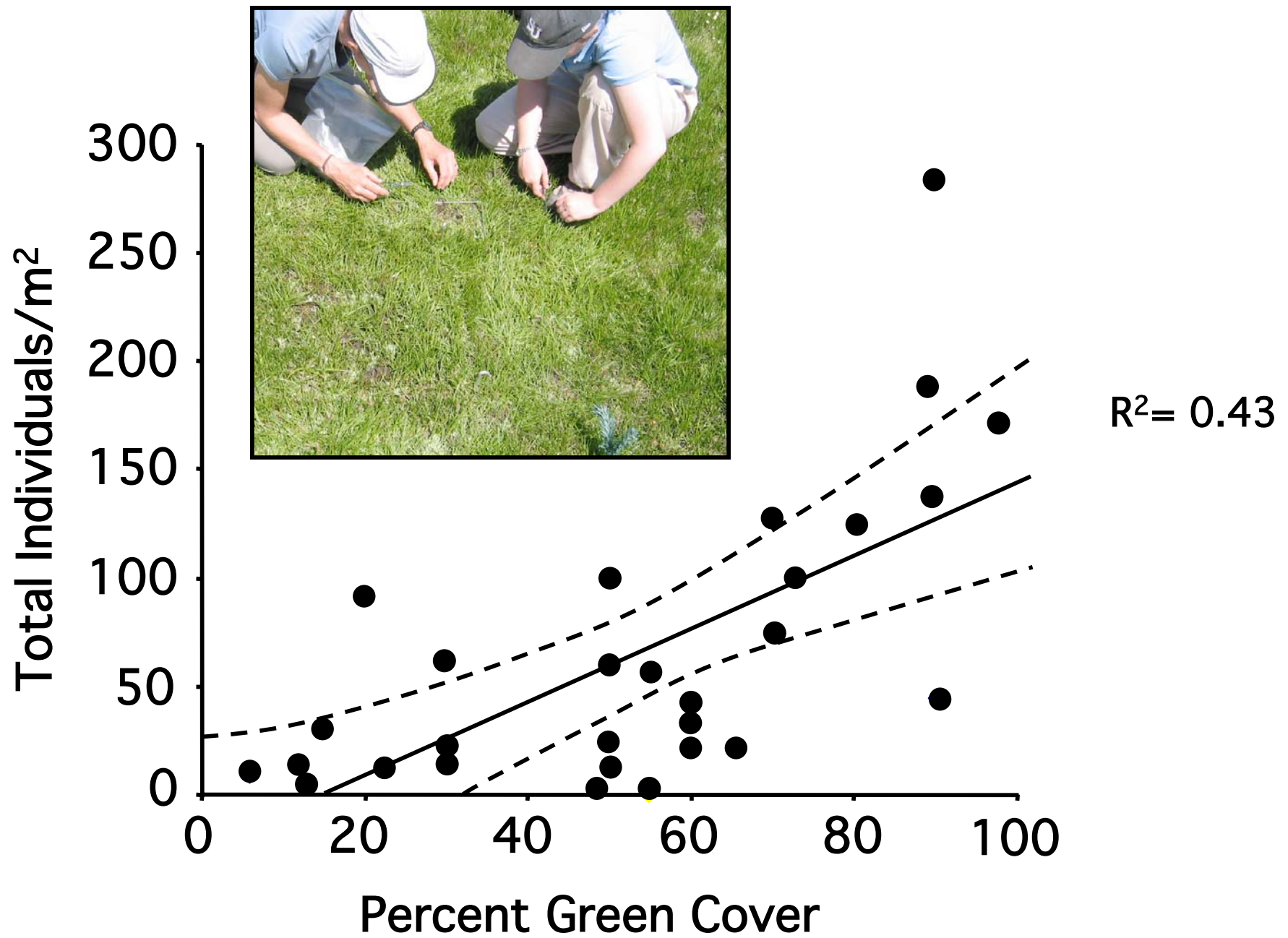


Fig. 43

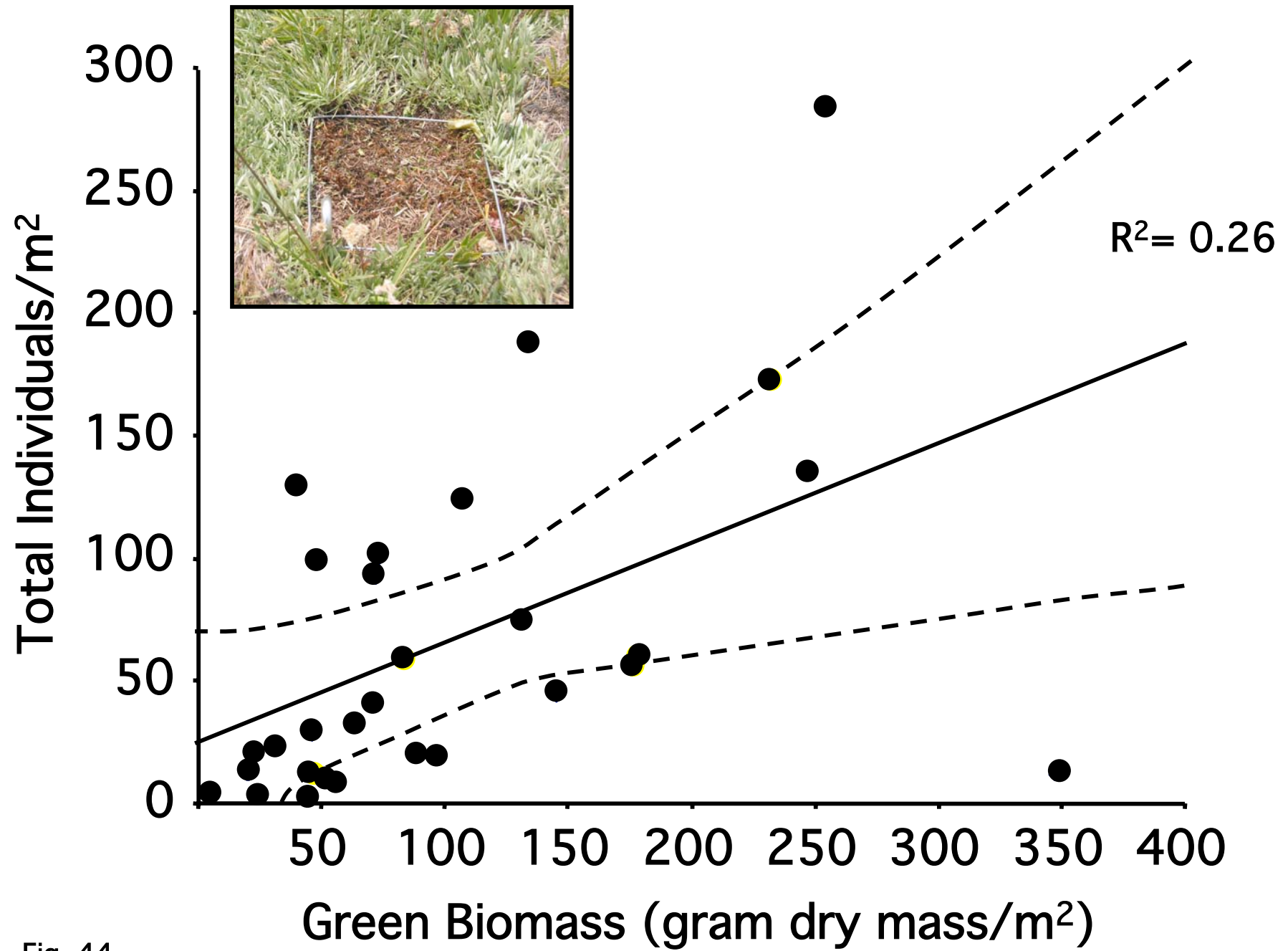


Fig. 44

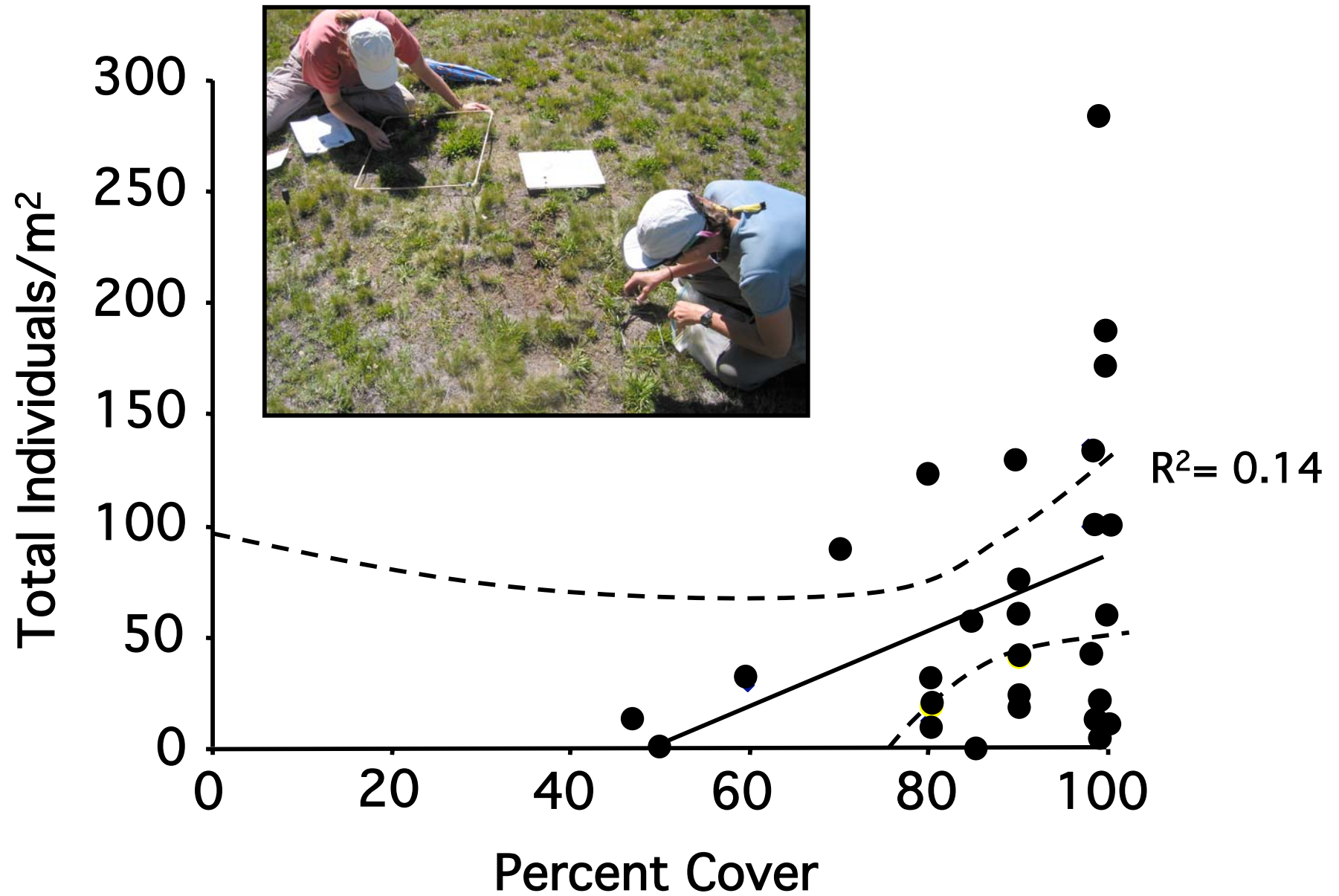


Fig. 45

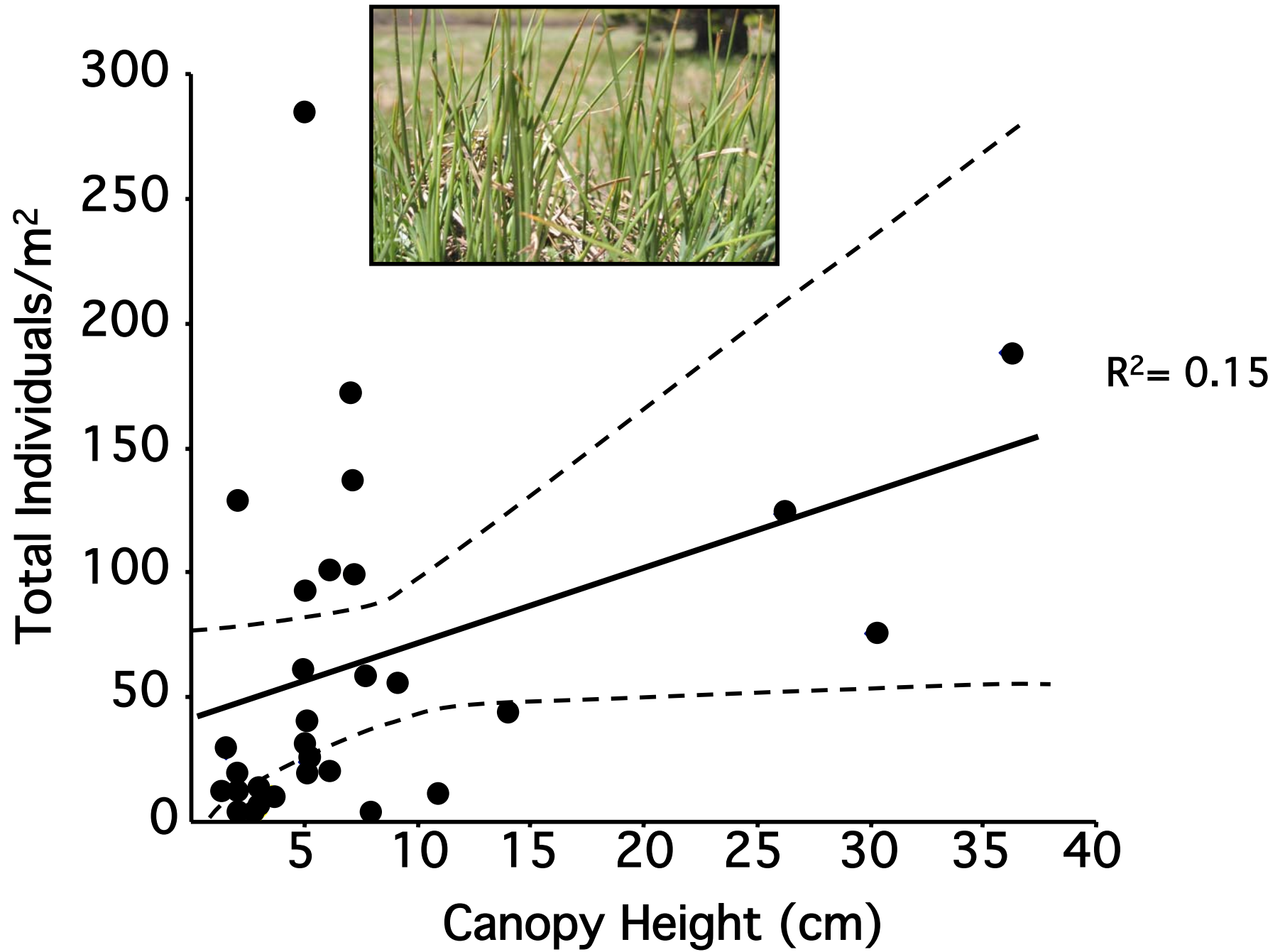


Fig. 46

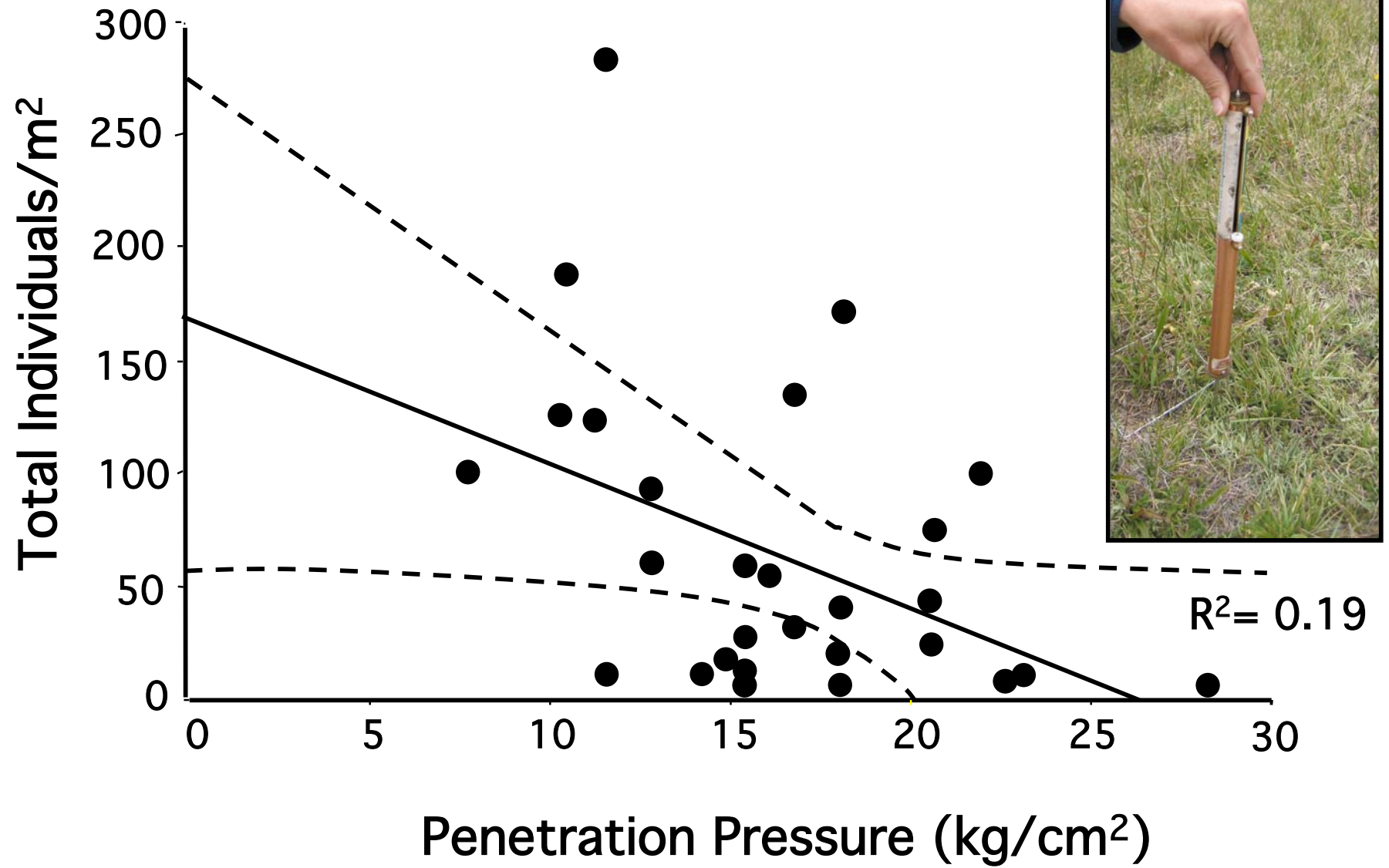


Fig. 47

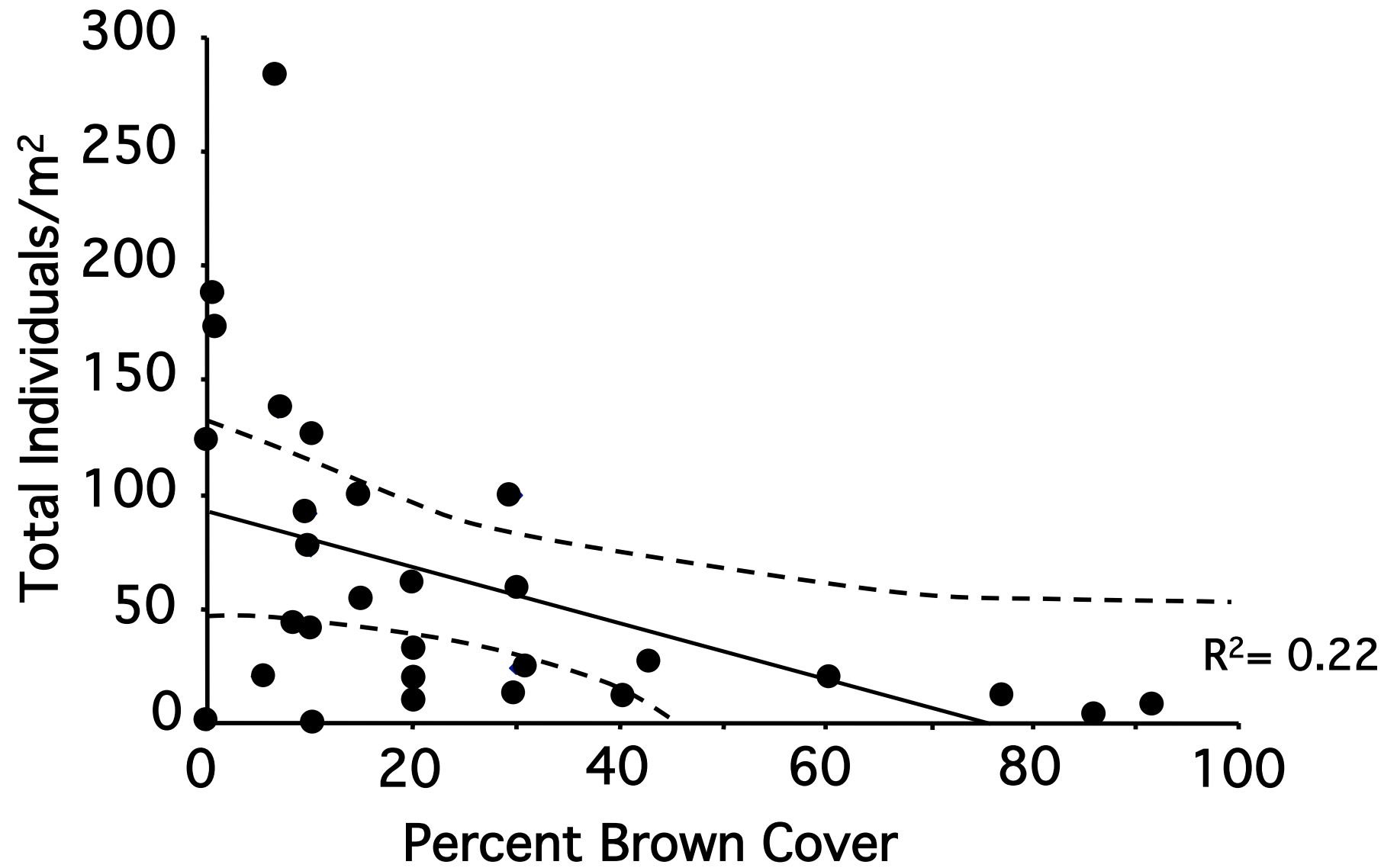


Fig. 48

Table 1. Sampling site numbers, dates, and UTM coordinates (WGS84, Zone 11) for 2004 Tuolumne samples. Continued next page.

Aquatic samples

04-1-1-1	13 May 04	290708	4194360
04-1-1-2	14 May 04	292157	4194249
04-1-1-3	14 May 04	291096	4194306
04-1-1-4	18 May 04	291372	4194239
04-1-1-5	18 May 04	290839	4194342
04-1-1-6	18 May 04	292104	4194135
04-1-1-7	30 May 04	291841	4194438
04-1-1-8	30 May 04	291059	4194510
04-1-1-9	30 May 04	291625	4194440
04-1-1-10	04 Jun 04	292162	4194285
04-1-1-11	04 Jun 04	292133	4194574
04-1-1-12	04 Jun 04	291723	4194141

Terrestrial samples

04-1-2-1	13 May 04	291179	4194301
04-1-2-2	13 May 04	291628	4194422
04-1-2-3	13 May 04	291744	4194180
04-1-2-4	18 May 04	290911	4194477
04-1-2-5	18 May 04	291904	4194262
04-1-2-6	18 May 04	291933	4194491
04-1-2-7	30 May 04	291899	4194601
04-1-2-8	30 May 04	290846	4194351
04-1-2-9	30 May 04	292260	4194596
04-1-2-10	04 Jun 04	290632	4194380
04-1-2-11	04 Jun 04	291593	4194268
04-1-2-12	04 Jun 04	291882	4194267
04-1-2-13	11 Jun 04	290986	4194372
04-1-2-14	11 Jun 04	290371	4194701
04-1-2-15	11 Jun 04	292109	4194290
04-1-2-16	18 Jun 04	291869	4194436
04-1-2-17	18 Jun 04	292316	4194577
04-1-2-18	18 Jun 04	291988	4194586
04-1-2-19	22 Jun 04	291438	4194228

Table 1 (cont.). Tuolumne 2004 sampling sites, dates, and UTM coordinates.

Terrestrial samples (cont.)

04-1-2-20	22 Jun 04	290365	4195050
04-1-2-21	22 Jun 04	292507	4194400
04-1-2-22	30 Jun 04	291613	4194319
04-1-2-23	30 Jun 04	291703	4194319
04-1-2-24	30 Jun 04	292627	4194390
04-1-2-25	16 Jul 04	291591	4194161
04-1-2-26	16 Jul 04	291829	4194332
04-1-2-27	16 Jul 04	291907	4194422
04-1-2-28	26 Jul 04	291067	4194351
04-1-2-29	26 Jul 04	290816	4194468
04-1-2-30	26 Jul 04	291126	4194493
04-1-2-31	10 Aug 04	291980	4194374
04-1-2-32	10 Aug 04	292133	4194207
04-1-2-33	10 Aug 04	292127	4194241
04-1-2-34	26 Aug 04	291899	4194604
04-1-2-35	26 Aug 04	292301	4194578
04-1-2-36	26 Aug 04	292055	4194621
04-1-2-37	10 Sep 04	292629	4194442
04-1-2-38	10 Sep 04	292175	4194680
04-1-2-39	10 Sep 04	290378	4194872
04-1-2-40	21 Sep 04	290676	4194385
04-1-2-41	21 Sep 04	291648	4194320
04-1-2-42	21 Sep 04	292218	4194330
04-1-2-43	05 Oct 04	291999	4194499
04-1-2-44	05 Oct 04	291185	4194474
04-1-2-45	05 Oct 04	290520	4194450
04-1-2-46	16 Oct 04	292172	4194373
04-1-2-47	16 Oct 04	290587	4194439
04-1-2-48	16 Oct 04	290587	4194439

Table 2. Sampling site numbers, dates, and UTM coordinates (WGS84, Zone 11) for 2005 Tuolumne samples. Continued next page.

Aquatic sites

05-1-1-1	10 Jun 05	292004	4194536
05-1-1-2	10 Jun 05	290628	4194565
05-1-1-3	10 Jun 05	290764	4194574
05-1-1-4	13 Jun 05	292091	4194486
05-1-1-5	13 Jun 05	291741	4194439
05-1-1-6	13 Jun 05	291391	4194362
05-1-1-7	22 Jun 05	292072	4194639
05-1-1-8	22 Jun 05	290680	4194640
05-1-1-9	27 Jun 05	290339	4195249
05-1-1-10	27 Jun 05	292038	4194525
05-1-1-11	05 Jul 05	291554	4194563
05-1-1-12	05 Jul 05	291651	4194423
05-1-1-13	18 Jul 05	290914	4194548
05-1-1-14	25 Jul 05	290986	4194547

Terrestrial sites

05-1-2-1	10 Jun 05	291389	4194419
05-1-2-2	10 Jun 05	291476	4194317
05-1-2-3	10 Jun 05	290770	4194642
05-1-2-4	13 Jun 05	291818	4194593
05-1-2-5	13 Jun 05	291741	4194503
05-1-2-6	13 Jun 05	291715	4194475
05-1-2-7	22 Jun 05	291717	4194484
05-1-2-8	22 Jun 05	291770	4194645
05-1-2-9	22 Jun 05	290498	4194639
05-1-2-10	27 Jun 05	291910	4194778
05-1-2-11	27 Jun 05	291525	4194524
05-1-2-12	27 Jun 05	291157	4194624
05-1-2-13	05 Jul 05	290924	4194588
05-1-2-14	05 Jul 05	290750	4194571
05-1-2-15	05 Jul 05	290515	4194624
05-1-2-16	11 Jul 05	290623	4194549

Table 2 (cont.). Tuolumne 2005 sampling sites, dates, and UTM coordinates.

Terrestrial samples (cont.)

05-1-2-17	11 Jul 05	290425	4194610
05-1-2-18	11 Jul 05	292015	4194809
05-1-2-19	18 Jul 05	291720	4194528
05-1-2-20	18 Jul 05	290944	4194709
05-1-2-21	25 Jul 05	291867	4194551
05-1-2-22	25 Jul 05	292539	4194495
05-1-2-23	01 Aug 05	292541	4194509
05-1-2-24	01 Aug 05	291081	4194709
05-1-2-25	31 Jul 05	292043	4194819
05-1-2-26	10 Aug 05	291389	4194411
05-1-2-27	10 Aug 05	292341	4194974
05-1-2-28	10 Aug 05	291842	4194691
05-1-2-29	15 Aug 05	291468	4194493
05-1-2-30	15 Aug 05	291789	4194486
05-1-2-31	15 Aug 05	291758	4194648
05-1-2-32	26 Aug 05	290698	4194633
05-1-2-33	26 Aug 05	290232	4194844
05-1-2-34	26 Aug 05	290516	4194632
05-1-2-35	07 Sep 05	292235	4194982
05-1-2-36	07 Sep 05	290693	4194601
05-1-2-37	07 Sep 05	291511	4194332
05-1-2-38	13 Sep 05	291754	4194635
05-1-2-39	13 Sep 05	291605	4194521
05-1-2-40	13 Sep 05	292075	4194813
05-1-2-41	06 Oct 05	290993	4194539
05-1-2-42	06 Oct 05	291316	4194353
05-1-2-43	06 Oct 05	290525	4194661
05-1-2-44	24 Oct 05	290459	4194620
05-1-2-45	24 Oct 05	291739	4194550
05-1-2-46	24 Oct 05	291541	4194433

Table 3. Sampling site numbers, dates, and UTM coordinates (WGS84, Zone 11) for 2005 Giant Forest samples. Continued next page.

Aquatic sites

05-2-1-1	18 May 05	343561	4046955
05-2-1-2	18 May 05	343996	4047107
05-2-1-3	19 May 05	344035	4047438
05-2-1-4	02 Jun 05	344023	4047022
05-2-1-5	02 Jun 05	343558	4046959
05-2-1-6	02 Jun 05	343996	4047090
05-2-1-7	16 Jun 05	343558	4046876
05-2-1-8	16 Jun 05	343581	4046839
05-2-1-9	16 Jun 05	343518	4047332
05-2-1-10	30 Jun 05	343543	4047224
05-2-1-11	30 Jun 05	343576	4046797
05-2-1-12	01 Jul 05	344003	4047023

Terrestrial sites

05-2-2-1	19 May 05	344147	4047521
05-2-2-2	19 May 05	344150	4047551
05-2-2-3	19 May 05	344138	4047556
05-2-2-4	19 May 05	343552	4047015
05-2-2-5	19 May 05	344059	4047476
05-2-2-6	19 May 05	343545	4047073
05-2-2-7	01 Jun 05	343540	4047017
05-2-2-8	01 Jun 05	343555	4047042
05-2-2-9	02 Jun 05	344129	4047527
05-2-2-10	02 Jun 05	344144	4047547
05-2-2-11	02 Jun 05	344145	4047533
05-2-2-12	02 Jun 05	344192	4047552
05-2-2-13	16 Jun 05	343089	4047358
05-2-2-14	16 Jun 05	343539	4047018
05-2-2-15	16 Jun 05	344135	4047544
05-2-2-16	16 Jun 05	344203	4047558
05-2-2-17	16 Jun 05	344129	4047553
05-2-2-18	16 Jun 05	344201	4047577

Table 3 (cont.). Giant Forest sampling sites, dates, and UTM coordinates.

Terrestrial samples (cont.)

05-2-2-19	30 Jun 05	343556	4047022
05-2-2-20	30 Jun 05	344173	4047556
05-2-2-21	30 Jun 05	344182	4047540
05-2-2-22	30 Jun 05	344198	4047579
05-2-2-23	30 Jun 05	344134	4047542
05-2-2-24	30 Jun 05	344169	4047516
05-2-2-25	28 Jul 05	344048	4047481
05-2-2-26	28 Jul 05	344123	4047534
05-2-2-27	28 Jul 05	343096	4047362
05-2-2-28	28 Jul 05	344167	4047561
05-2-2-29	28 Jul 05	343553	4047110
05-2-2-30	28 Jul 05	344178	4047521
05-2-2-31	25 Aug 05	343103	4047357
05-2-2-32	25 Aug 05	343098	4047348
05-2-2-33	25 Aug 05	344006	4047367
05-2-2-34	25 Aug 05	344005	4047267
05-2-2-35	25 Aug 05	344098	4047493
05-2-2-36	25 Aug 05	344014	4047058
05-2-2-37	29 Sep 05	344178	4047498
05-2-2-38	29 Sep 05	344005	4047382
05-2-2-39	29 Sep 05	344124	4047533
05-2-2-40	29 Sep 05	344190	4047556
05-2-2-41	29 Sep 05	344001	4047047
05-2-2-42	29 Sep 05	343554	4047174
05-2-2-43	26 Oct 05	344065	4047301
05-2-2-44	26 Oct 05	343538	4047262
05-2-2-45	26 Oct 05	344071	4047323
05-2-2-46	26 Oct 05	343095	4047351
05-2-2-47	26 Oct 05	343552	4047148
05-2-2-48	26 Oct 05	344182	4047467

Table 4. Densities (per m²; SE) and frequency of occurrence of taxa in aquatic samples. Blanks, rather than “zeros,” are used to indicate that a given taxon was not collected. “Unidentified Diptera” were too badly damaged for taxonomic work. Gastropod and bivalve family identifications are pending confirmation by specialists. Continued next page.

	Tuolumne 04 (n=12)			Tuolumne 05 (n=14)			Giant Forest 05 (n=12)		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Mollusca: Gastropoda									
Basommatophora				0.25	(0.25)	0.071	0.74	(0.34)	0.33
Lancidae				0.25	(0.25)	0.071			
Lymnaeidae?							0.74	(0.34)	0.33
Mollusca: Bivalvia									
Veneroida							16	(11)	0.42
Sphaeriidae							16	(11)	0.42
Hexapoda									
Collembola	0.15	(0.15)	0.083				1.3	(1.2)	0.17
Entomobryidae	0.15	(0.15)	0.083						
Isotomidae							1.3	(1.2)	0.17

Table 4 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in aquatic samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Ephemeroptera	449	(414)	0.58	128	(100)	0.57	48	(24)	0.75
Baetidae							0.15	(0.15)	0.083
Ephemerellidae							0.15	(0.15)	0.083
Heptageniidae							0.15	(0.15)	0.083
Leptophlebiidae							2.2	(2.2)	0.083
Siphonuridae	449	(414)	0.58	128	(100)	0.57	45	(24)	0.75
Odonata	1.2	(0.55)	0.33	3.6	(2.3)	0.29	0.30	(0.30)	0.083
Anisoptera									
Libellulidae	0.30	(0.30)	0.083				0.30	(0.30)	0.083
Zygoptera									
Lestidae	0.89	(0.51)	0.25	3.6	(2.3)	0.29			
Plecoptera	0.15	(0.15)	0.083				53	(25)	0.75
Nemouridae							45	(24)	0.75
Leuctridae							7.4	(4.8)	0.25
Chloroperlidae	0.15	(0.15)	0.083						
Hemiptera	0.59	(0.59)	0.083	5.0	(2.1)	0.36	2.5	(2.4)	0.17
Corixidae	0.59	(0.59)	0.083	3.8	(1.6)	0.36			
Notonectidae				1.2	(0.69)	0.14	2.5	(2.4)	0.17

Table 4 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in aquatic samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Coleoptera	30	(11)	0.92	9.4	(2.8)	0.64	7.3	(1.4)	0.92
Dytiscidae	17.5	(8.5)	0.75	6.1	(2.0)	0.57	3.4	(1.3)	0.50
Hydrophilidae	8.5	(3.7)	0.5	3.1	(2.1)	0.21			
Hydraenidae	3.6	(1.5)	0.50	0.13	(0.13)	0.071			
Scirtidae							0.44	(0.44)	0.083
Chrysomelidae							3.4	(1.4)	0.66
Trichoptera	3.1	(2.3)	0.42	0.64	(0.51)	0.14	3.1	(1.5)	0.50
Polycentropodidae							0.15	(0.15)	0.083
Limnephilidae	3.1	(2.3)	0.42	0.64	(0.51)	0.14	2.4	(1.5)	0.42
Brachycentridae							0.59	(0.46)	0.17
Diptera	761	(391)	0.92	735	(473)	1.0	76	(31)	1.0
Tipulidae							1.5	(0.48)	0.50
Ceratopogonidae							0.89	(0.51)	0.25
Chironomidae	26	(10)	0.75	58	(26)	0.71	29	(9.6)	0.92
Culicidae	675	(397)	0.92	675	(478)	0.79	9	(8.6)	0.17
Dixidae				1.8	(1.3)	0.14	3.1	(2.1)	0.25
Simuliidae							31	(26)	0.58
Bibionidae	59	(51)	0.42						
Tabanidae							0.59	(0.33)	0.25
Unidentified							0.44	(0.32)	0.17
Chelicerata									
Acari	2.1	(0.75)	0.58	2.0	(1.1)	0.29	7.7	(2.9)	0.75

Table 5. Densities (per m²; SE) and frequency of occurrence of taxa in terrestrial samples. Blanks, rather than “zeros,” are used to indicate that a given taxon was not collected. “Unidentified” fauna were too badly damaged or too small for taxonomic work. Gastropoda, Diplopoda, and Acari family identifications are pending confirmation by specialists. Continued next page.

	Tuolumne 04 (n=48)		Tuolumne 05 (n=46)		Giant Forest 05 (n=48)	
	Mean	(SE) Freq.	Mean	(SE) Freq.	Mean	(SE) Freq.
Mollusca: Gastropoda					9.9	(4.2) 0.29
Pulmonata					2.1	(0.88) 0.15
Basommatophora					7.8	(3.4) 0.27
Mollusca: Bivalvia						
Veneroida						
Sphaeriidae					2.5	(2.5) 0.021
Myriapoda: Diplopoda					0.25	(0.18) 0.042
Spirobolida					0.17	(0.17) 0.021
Julida					0.083	(0.083) 0.021

Table 5 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in terrestrial samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Hexapoda									
Collembola	0.083	(0.083)	0.021				3.3	(2.1)	0.19
Entomobryidae	0.083	(0.083)	0.021						
Isotomidae							3.3	(2.1)	0.19
Orthoptera	0.25	(0.18)	0.042	0.43	(0.22)	0.087			
Acrididae	0.25	(0.18)	0.042	0.43	(0.22)	0.087			
Hemiptera	0.33	(0.20)	0.062	1.7	(0.59)	0.26	25	(5.1)	0.90
Saldidae				0.35	(0.35)	0.022	0.42	(0.34)	0.042
Miridae				0.17	(0.12)	0.043	5.9	(1.9)	0.40
Nabidae	0.083	(0.083)	0.021	0.35	(0.21)	0.065	4.2	(1.1)	0.38
Anthocoridae							0.17	(0.12)	0.042
Pentatomidae	0.083	(0.083)	0.021				0.25	(0.14)	0.062
Lygaeidae	0.17	(0.17)	0.021	0.87	(0.39)	0.15	11	(3.9)	0.48
Unidentified							2.5	(1.7)	0.10
Homoptera	5.3	(3.02)	0.31	9.1	(2.5)	0.50	287	(33)	1.0
Auchenorrhyncha									
Cicadellidae	4.5	(2.6)	0.25	7.3	(2.0)	0.44	197	(29)	1.0
Delphacidae	0.42	(0.34)	0.042	1.6	(0.58)	0.20	82	(16)	0.83
Sternorrhyncha									
Psyllidae	0.33	(0.16)	0.083	0.17	(0.12)	0.043	2.0	(1.0)	0.13
Aphididae				0.087	(0.087)	0.022	6.3	(1.7)	0.35

Table 5 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in terrestrial samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Coleoptera	3.6	(0.86)	0.44	3.5	(0.83)	0.39	82	(16)	0.98
Carabidae	0.58	(0.27)	0.10	0.35	(0.21)	0.065	4.0	(0.96)	0.35
Hydrophilidae							0.25	(0.18)	0.15
Ptiliidae							4.3	(3.0)	0.083
Staphylinidae				0.78	(0.41)	0.11	33	(8.8)	0.73
Scarabaeidae	0.83	(0.39)	0.13	0.61	(0.25)	0.13			
Buprestidae	0.083	(0.083)	0.021				0.083	(0.083)	0.021
Throscidae	0.083	(0.083)	0.021				0.75	(0.67)	0.042
Elateridae	0.083	(0.083)	0.021	0.43	(0.36)	0.043	0.25	(0.18)	0.042
Cantharidae							1.1	(0.44)	0.15
Trogossitidae							0.17	(0.17)	0.021
Cleridae							0.17	(0.17)	0.021
Sphindidae							0.17	(0.17)	0.021
Phalacridae				0.087	(0.087)	0.022	0.17	(0.12)	0.042
Coccinellidae	0.58	(0.31)	0.083	0.35	(0.17)	0.087	5.3	(2.2)	0.33
Latriidae							16	(3.8)	0.58
Mordellidae				0.087	(0.087)	0.022	0.33	(0.33)	0.021
Anthicidae	0.67	(0.30)	0.13	0.35	(0.27)	0.043	15	(4.2)	0.50
Cerambycidae							0.17	(0.17)	0.021
Chrysomelidae	0.33	(0.16)	0.083	0.43	(0.22)	0.087	0.17	(0.17)	0.021
Curculionidae	0.33	(0.16)	0.083				0.33	(0.33)	0.021
Unidentified							0.25	(0.14)	0.063

Table 5 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in terrestrial samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Hymenoptera	9.5	(2.2)	0.52	12	(3.0)	0.57	37	(6.7)	0.81
Tenthredinidae	0.083	(0.083)	0.021				0.17	(0.17)	0.021
Ceraphronidae							0.33	(0.20)	0.062
Braconidae	0.083	(0.083)	0.021	0.96	(0.33)	0.20	24	(6.3)	0.69
Ichneumonidae	0.92	(0.46)	0.13	0.17	(0.12)	0.043	1.6	(0.60)	0.17
Mymaridae	0.083	(0.083)	0.021				0.33	(0.20)	0.062
Pteromalidae				0.17	(0.12)	0.043	4.6	(1.4)	0.31
Figitidae							0.083	(0.083)	0.021
Proctotrupidae							0.17	(0.17)	0.021
Diapriidae				0.087	(0.087)	0.022	0.58	(0.38)	0.062
Scelionidae							0.17	(0.17)	0.021
Platygastridae							0.083	(0.083)	0.021
Sphecidae	0.083	(0.083)	0.021						
Colletidae	0.083	(0.083)	0.021						
Pompilidae							0.083	(0.083)	0.021
Formicidae	8.3	(2.1)	0.50	11	(2.8)	0.50	5.0	(1.5)	0.29
Lepidoptera	1.6	(0.55)	0.21	1.4	(0.45)	0.22	1.7	(0.69)	0.17
Acanthopteroctetidae				0.52	(0.27)	0.087	0.083	(0.083)	0.021
Gracillariidae				0.087	(0.087)	0.022			
Elachistidae				0.087	(0.087)	0.022			
Coleophoridae	0.67	(0.32)	0.10				0.083	(0.083)	0.021
Gelechiidae	0.67	(0.32)	0.10	0.26	(0.15)	0.065			
Pyralidae	0.25	(0.18)	0.042				0.17	(0.12)	0.042

Table 5 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in terrestrial samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Lepidoptera, cont.									
Crambidae				0.26	(0.15)	0.065			
Noctuidae							0.67	(0.38)	0.083
Unidentified				0.17	(0.12)	0.043	0.67	(0.47)	0.042
Diptera	4.3	(1.1)	0.42	29	(9.6)	0.61	1721	(366)	1.0
Nematocera									
Tipulidae							0.083	(0.083)	0.021
Psychodidae							0.25	(0.25)	0.021
Ceratopogonidae	0.25	(0.18)	0.042	0.17	(0.17)	0.022	0.67	(0.36)	0.10
Chironomidae	0.083	(0.083)	0.021	0.35	(0.21)	0.065	0.50	(0.37)	0.042
Culicidae	0.083	(0.083)	0.021	0.17	(0.12)	0.043	0.17	(0.17)	0.021
Bibionidae	0.083	(0.083)	0.021						
Cecidomyiidae	0.17	(0.12)	0.042				0.25	(0.25)	0.021
Mycetophylidae	0.083	(0.083)	0.021	0.087	(0.087)	0.022	1.3	(0.72)	0.10
Scatopsidae	0.083	(0.083)	0.021				0.083	(0.083)	0.021
Sciaridae	0.25	(0.18)	0.042	2.7	(1.1)	0.17	4.1	(1.1)	0.31
Brachycera									
Athericidae				0.087	(0.087)	0.022	0.33	(0.33)	0.021
Empididae				0.26	(0.19)	0.043	12	(4.5)	0.38
Dolichopodidae	0.17	(0.12)	0.042	0.52	(0.27)	0.087	2.3	(1.2)	0.13
Lonchopteridae				3.3	(1.7)	0.15	10	(3.2)	0.40
Pipunculidae							0.17	(0.17)	0.021
Phoridae	0.083	(0.083)	0.021	0.96	(0.48)	0.13	3.4	(1.2)	0.29

Table 5 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in terrestrial samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Diptera, cont.									
Anthomyiidae	1.1	(0.46)	0.19	3.0	(0.87)	0.33	1.9	(0.57)	0.23
Hippoboscidae	0.083	(0.083)	0.021						
Muscidae	0.083	(0.083)	0.021	0.43	(0.22)	0.087	4.0	(1.2)	0.35
Tachinidae	0.083	(0.083)	0.021						
Tephritidae	0.083	(0.083)	0.021	0.087	(0.087)	0.022	0.50	(0.37)	0.042
Sepsidae	0.083	(0.083)	0.021	0.35	(0.21)	0.065	13	(2.7)	0.52
Clusiidae	0.083	(0.083)	0.021						
Chloropidae	1.2	(0.46)	0.15	1.1	(0.52)	0.13	21	(6.8)	0.48
Heleomyzidae							0.92	(0.49)	0.083
Sphaeroceridae	0.33	(0.20)	0.062	13	(6.0)	0.37	1482	(343)	1.0
Diastatidae							1.3	(0.68)	0.10
Drosophilidae				0.52	(0.24)	0.11	154	(38)	0.83
Ephydridae				1.2	(0.64)	0.11	5.3	(1.4)	0.31
Unidentified				0.087	(0.087)	0.022	1.2	(0.62)	0.10

Table 5 (cont.). Densities (per m²; SE) and frequency of occurrence of taxa in terrestrial samples.

	Tuolumne 04			Tuolumne 05			Giant Forest 05		
	Mean	(SE)	Freq.	Mean	(SE)	Freq.	Mean	(SE)	Freq.
Chelicerata									
Araneae	3.4	(0.93)	0.40	15	(6.8)	0.50	51	(6.2)	0.94
Araneidae	0.25	(0.14)	0.062				0.25	(0.18)	0.042
Tetragnathidae	0.083	(0.083)	0.021	0.087	(0.087)	0.022	1.3	(1.1)	0.062
Linyphiidae	0.83	(0.43)	0.10	8.5	(3.3)	0.44	25	(4.3)	0.75
Dictynidae							1.3	(0.72)	0.13
Agelenidae	0.33	(0.16)	0.083	0.087	(0.087)	0.022	0.50	(0.50)	0.021
Oxyopidae				0.087	(0.087)	0.022			
Pisauridae							0.17	(0.12)	0.042
Lycosidae	0.42	(0.21)	0.083	1.2	(0.39)	0.22	6.0	(1.8)	0.33
Clubionidae	0.083	(0.083)	0.021				0.58	(0.29)	0.083
Anyphaenidae				3.1	(3.0)	0.043	5.3	(1.4)	0.35
Gnaphosidae	0.25	(0.18)	0.042	0.26	(0.19)	0.043	2.5	(1.2)	0.17
Philodromidae				0.087	(0.087)	0.022	2.0	(0.64)	0.21
Thomisidae	0.75	(0.33)	0.13	1.5	(0.44)	0.24	4.7	(1.2)	0.33
Salticidae	0.42	(0.18)	0.10	0.17	(0.12)	0.043	0.92	(0.68)	0.083
Unidentified							0.083	(0.083)	0.021
Acari	20	(5.6)	0.46	10	(3.2)	0.48	40	(9.4)	0.73

Table 6. Summary of coarse aquatic vegetation and physical data. Blanks indicate that certain metrics were not collected in 2004.

	Tuolumne 04 (n=12)		Tuolumne 05 (n=14)		Giant Forest (n=12)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
Percent bare substrate	19	(7.1)	49	(11)	0.83	(0.83)
Percent green cover	24	(2.0)	16	(5.3)	57	(8.7)
Percent brown cover	25	(4.3)	8.4	(2.8)	15	(4.3)
Percent litter cover	33	(4.4)	22	(7.2)	28	(5.2)
Canopy height (cm)	14	(2.4)	11	(4.1)	41	(5.3)
Litter depth (cm)			5.6	(2.1)	7.5	(0.83)
Live biomass (gdm/m ²)	120	(29)	50	(22)	527	(114)
Dead biomass (gdm/m ²)	384	(101)	182	(55)	703	(146)
Patch size (m ²)	150	(70)	207	(68)	18700	(4960)
Water temperature (°C)	15	(1.9)	16	(1.6)	13	(0.89)
Water depth (cm)	14	(2.6)	16	(2.2)	15	(2.7)
Flow (m/sec)			0.0036	(0.0023)	0.038	(0.014)

Table 7. Summary of coarse terrestrial vegetation and physical data. Blanks indicate that certain metrics were not collected in 2004.

	Tuolumne 04 (n=48)		Tuolumne 05 (n=46)		Giant Forest (n=48)	
	Mean	(SE)	Mean	(SE)	Mean	(SE)
Percent bare ground	10	(1.5)	11	(1.6)	2.8	(1.0)
Percent green cover	46	(3.8)	61	(4.4)	59	(4.6)
Percent brown cover	29	(3.6)	19	(3.7)	16	(2.9)
Percent litter cover	15	(1.8)	10	(1.6)	22	(3.0)
Canopy height (cm)	8.9	(1.1)	8.1	(1.0)	49	(4.8)
Litter depth (cm)			1.0	(0.18)	7.8	(0.64)
Live biomass (gdm/m ²)	109	(13)	127	(13)	222	(27)
Dead biomass (gdm/m ²)	194	(18)	264	(69)	570	(42)
Patch size (m ²)	19700	(7220)	37200	(15300)	48700	(8740)
Air temperature (°C)	19	(0.75)	20	(0.60)	19	(0.91)
Ground temperature (°C)			22	(0.58)	21	(1.0)
Relative humidity (%)			39	(2.3)	53	(1.8)
Wind speed (km/hr)			9.2	(0.64)	3.1	(0.34)
Penetration pressure (kg/cm ²)	16	(0.76)	12	(0.76)	6.8	(0.34)
Soil moisture (% mass)			42	(2.4)	60	(3.8)

Table 8. Summary of results of all possible multiple regression models of Tuolumne aquatic faunal order and total abundances on physical and coarse vegetation predictor variables. Positive or negative relationships indicate whether a given predictor was entered into a final model at “p” < 0.025 with a positive or negative coefficient (“+” or “-,” respectively). Predictors could not be successfully entered into models for true bugs or mites.

Response Variables

	Mayflies	Beetles	Caddisflies	Flies	Total
R²	0.98	0.20	0.99	0.40	0.39

Predictors

Water Depth	-	-	+	-	-
Water Flow	+		-		
Canopy Height	-				
Percent Green Cover	+	+	-		
Percent Brown Cover	+		-		
Total Percent Cover	+				
Green Standing Crop			+		
Litter Mass		+	-	+	+
Percent Litter	+				
Litter Depth	-		+		
Patch Size	-		+		

Entered variable without significant effects on models:

Water Temperature

Table 9. Mean percent (SE) cover of vegetation and frequency of occurrence in Tuolumne flooded plots. Blanks, rather than “zeros,” are used to indicate that a given taxon was not collected. “NA” indicates that a species was recorded as “< 1% cover” for all plots in which the species occurred. Continued next page.

	Tuolumne 04 (n=12)			Tuolumne 05 (n=14)		
	Mean	(SE)	Frequency	Mean	(SE)	Frequency
Isoetaceae						
<i>Isoetes</i> sp.	0.083	(0.083)	0.083	0.14	(0.10)	0.14
Asteraceae						
<i>Oreostemma alpigenus</i>				0.14	(0.10)	0.14
Caryophyllaceae						
<i>Stellaria longipes</i>				0.071	(0.071)	0.071
Ericaceae						
<i>Vaccinium caespitosum</i>	0.17	(0.17)	0.083	0.071	(0.071)	0.071
Fabaceae						
<i>Lupinus lepidus</i>				0.071	(0.071)	0.071
Gentianaceae						
<i>Gentiana newberryi</i>	0.083	(0.083)	0.083	0.071	(0.071)	0.071
<i>Gentianopsis holopetala</i>				0.071	(0.071)	0.071
<i>Gentiana/Gentianopsis</i>	NA		0.17			
Hypericaceae						
<i>Hypericum anagalloides</i>	0.17	(0.11)	0.083			
Polygonaceae						
<i>Polygonum bistortoides</i>	NA		0.083	0.071	(0.071)	0.071
Primulaceae						
<i>Dodecatheon</i> sp.	NA		0.083	0.071	(0.071)	0.071
Ranunculaceae						
<i>Ranunculus aquatilis</i>	1.7	(1.7)	0.083	0.071	(0.071)	0.071
Salicaceae						
<i>Salix</i> spp. (some <i>planifolia</i>)	0.92	(0.56)	0.25	1.2	(1.2)	0.21
Cyperaceae						
<i>Carex utriculata</i>	24	(9.7)	0.75	16	(7.9)	0.57
<i>Carex subnigricans</i>				0.071	(0.071)	0.071

Table 9 (cont.). Mean percent (SE) cover of vegetation and frequency of occurrence in Tuolumne flooded plots.

	Tuolumne 04			Tuolumne 05		
	Mean	(SE)	Frequency	Mean	(SE)	Frequency
Poaceae						
<i>Calamagrostis breweri</i>				1.4	(1.4)	0.071
<i>Deschampsia cespitosa</i>	3.2	(1.7)	0.42	0.21	(0.15)	0.14
<i>Ptilagrostis kingii</i>				0.50	(0.37)	0.14

Table 10. Summary of results of all possible multiple regression models of Giant Forest aquatic faunal order and total abundances on physical and coarse vegetation predictor variables. Positive or negative relationships indicate whether a given predictor was entered into a final model at “p” < 0.025 with a positive or negative coefficient (“+” or “-,” respectively). Predictors could not be successfully entered into models for mayflies, beetles, mites, snails, clams, or total individuals.

Response Variables

	Stoneflies	True bugs	Caddisflies	Flies
R²	0.36	0.99	0.40	0.43

Predictors

Water Temperature			+	
Canopy Height				+
Percent Brown Cover		-		
Total Percent Cover		-		
Percent Litter	+			
Litter Depth		+		
Patch Size		+		

Entered variables without significant effects on models:

Water Depth
 Water Flow
 Percent Green Cover
 Green Standing Crop
 Litter Mass

Table 11. Mean percent (SE) cover of vegetation and frequency of occurrence in Giant Forest flooded plots (n=12). Blanks, rather than “zeros,” are used to indicate that a given taxon was not collected.

	Mean	SE	Frequency
Equisetaceae			
<i>Equisetum arvense</i>	0.42	(0.26)	0.25
<i>Equisetum</i> sp.	0.083	(0.083)	0.083
Apiaceae			
<i>Oxyopolis occidentalis</i>	18	(5.5)	0.75
Polygonaceae			
<i>Polygonum bistortoides</i>	0.25	(0.13)	0.25
Primulaceae			
<i>Dodecatheon redolens</i>	0.083	(0.083)	0.083
Cyperaceae			
<i>Carex aquatilis</i>	0.42	(0.42)	0.083
<i>Carex nebrascensis</i>	2.8	(2.1)	0.33
<i>Carex utriculata</i>	9.0	(4.0)	0.42
<i>Eleocharis</i> sp.	3.5	(3.3)	0.25
<i>Scirpus congdonii</i>	4.2	(3.4)	0.17
<i>Scirpus microcarpus</i>	3.3	(2.3)	0.17
<i>Scirpus</i> sp.	2.5	(1.8)	0.17
Liliaceae			
<i>Camassia quamash</i>	0.083	(0.083)	0.083

Table 12. Summary of results of all possible multiple regression models of Tuolumne terrestrial faunal order and total abundances on physical and coarse vegetation predictor variables. A “+” indicates that a given predictor was entered into a final model at $p < 0.025$; there were no significant negative coefficients. Predictors could not be successfully entered into models for beetles, or ants/wasps.

	Response Variables						
	True bugs	Leafhoppers	Moths	Flies	Spiders	Mites	Total
R²	0.29	0.22	0.17	0.15	0.14	0.12	0.17
Predictors							
Soil Moisture			+	+		+	
Canopy Height	+				+		
Green Standing Crop		+					+

Entered variables without significant effects on models:

Percent Green Cover
 Percent Brown Cover
 Percent Litter
 Total Percent Cover
 Litter mass
 Litter Depth
 Patch Size
 Air Temperature
 Ground Temperature
 Relative Humidity
 Wind Speed
 Water Table Depth
 Soil Penetration Pressure

Table 13. Mean percent (SE) cover of vegetation and frequency of occurrence in Tuolumne terrestrial plots. Blanks, rather than “zeros,” are used to indicate that a given taxon was not collected. “NA” indicates that a species was recorded as “< 1% cover” for all plots in which the species occurred. Continued next page.

	Tuolumne 04 (n=48)			Tuolumne 05 (n=46)		
	Mean	(SE)	Frequency	Mean	(SE)	Frequency
Ophioglossaceae						
<i>Botrychium simplex</i>	0.063	(0.035)	0.062			
Pinaceae						
<i>Pinus contorta</i>	0.021	(0.021)	0.021			
Asteraceae						
<i>Achillea millefolium</i>	0.063	(0.046)	0.042			
<i>Agoseris glauca</i>	0.021	(0.021)	0.021			
<i>Antennaria</i> spp., (mostly <i>corymbosa</i>)	10	(2.5)	0.79	9.6	(1.7)	0.76
<i>Oreostemma alpigenus</i>	3.0	(1.5)	0.38	0.80	(0.25)	0.41
<i>Oreostemma occidentalis</i>				0.15	(0.150)	0.022
<i>Oreostemma</i> sp.	NA		0.021			
<i>Microseris</i> sp.	0.042	(0.042)	0.021			
<i>Solidago multiradiata</i>	0.23	(0.17)	0.083	0.96	(0.54)	0.15
Caryophyllaceae						
<i>Stellaria</i> sp., cf. <i>longipes</i> , <i>umbellata</i>	0.13	(0.048)	0.13	0.24	(0.064)	0.24
Ericaceae						
<i>Vaccinium</i> spp. (mostly <i>caespitosum</i>)	1.1	(0.48)	0.17	1.6	(0.62)	0.26
Fabaceae						
<i>Lupinus</i> sp.	0.10	(0.10)	0.021			
<i>Trifolium</i> sp., cf. <i>monanthum</i>	0.29	(0.12)	0.17	0.28	(0.15)	0.11
Gentianaceae (including <i>Gentiana newberryi</i> and <i>Gentianopsis holopetala</i>)	0.90	(0.43)	0.27	0.30	(0.10)	0.24
Hypericaceae						
<i>Hypericum anagalloides</i>	0.021	(0.021)	0.021	0.065	(0.037)	0.065

Table 13 (cont.). Mean percent (SE) cover of vegetation and frequency of occurrence in Tuolumne terrestrial plots. Continued next page.

	Tuolumne 04			Tuolumne 05		
	Mean	(SE)	Frequency	Mean	(SE)	Frequency
Onagraceae						
<i>Epilobium</i> sp.,						
cf. <i>phalleanum</i>	0.063	(0.035)	0.062	0.065	(0.048)	0.043
<i>Gayophytum</i> sp.	0.042	(0.029)	0.042			
Polygonaceae						
<i>Polygonum bistortoides</i>	1.3	(0.38)	0.38	3.5	(1.0)	0.33
<i>Polygonum polygaloides</i>				0.043	(0.043)	0.022
<i>Rumex paucifolius</i>	0.13	(0.057)	0.10	0.28	(0.13)	0.15
Portulacaceae						
<i>Lewisia</i> sp. (one						
occurrence <i>pygmaea</i>)	0.021	(0.021)	0.021	0.043	(0.030)	0.043
Primulaceae						
<i>Dodecatheon</i> sp.,						
cf. <i>subalpinum</i>	0.85	(0.35)	0.21	1.9	(1.1)	0.20
Ranunculaceae						
<i>Ranunculus</i> sp.				.065	(0.048)	0.043
Rosaceae						
<i>Fragaria virginiana</i>	0.063	(0.063)	0.021			
<i>Ivesia lycopodioides</i>	0.67	(0.18)	0.29	0.67	(0.18)	0.39
<i>Potentilla</i> sp.	0.15	(0.094)	0.062	0.065	(0.065)	0.022
<i>Sibbaldia procumbens</i>				0.065	(0.065)	0.022
Rubiaceae						
<i>Galium trifidum</i>	0.021	(0.021)	0.021	0.022	(0.022)	0.022
Salicaceae						
<i>Salix eastwoodiae?</i>				0.065	(0.065)	0.022
Saxifragaceae						
<i>Saxifraga</i> sp.,						
cf. <i>bryophora</i>	0.31	(0.25)	0.062			
Scrophulariaceae						
<i>Castilleja lemmonii</i>	0.13	(0.11)	0.021			
<i>Mimulus primuloides</i>	0.10	(0.054)	0.083	0.63	(0.44)	0.13
<i>Penstemon heterodoxus</i>	0.44	(0.20)	0.17	0.24	(0.16)	0.065

Table 13 (cont.). Mean percent (SE) cover of vegetation and frequency of occurrence in Tuolumne terrestrial plots.

	Tuolumne 04			Tuolumne 05		
	Mean	(SE)	Frequency	Mean	(SE)	Frequency
Violaceae						
<i>Viola</i> spp., (mostly <i>adunca</i> , one occurrence <i>macloskeyi</i>)	0.77	(0.36)	0.25	0.28	(0.086)	0.24
Cyperaceae						
<i>Carex filifolia</i>	1.7	(0.85)	0.17	1.2	(0.88)	0.087
<i>Carex rossii</i>	0.10	(0.09)	0.021	0.5	(0.27)	0.15
<i>Carex subnigricans</i>	0.29	(0.15)	0.13	0.20	(0.059)	0.20
<i>Carex utriculata</i>	0.17	(0.17)	0.042	3.0	(2.2)	0.065
<i>Carex</i> sp.	2.3	(1.02)	0.33	0.28	(0.13)	0.13
<i>Eleocharis acicularis</i>				0.11	(0.11)	0.022
<i>Scirpus clementis</i>	0.083	(0.050)	0.062	0.087	(0.068)	0.043
Juncaceae						
<i>Juncus</i> spp. (mostly <i>balticus</i> , one occurrence <i>orthophyllus</i>)	1.8	(1.03)	0.35	1.5	(0.63)	0.33
<i>Luzula comosa</i>				0.022	(0.022)	0.022
<i>Luzula</i> spp. (mostly <i>orestera</i>)	0.25	(0.10)	0.15			
Poaceae						
<i>Calamagrostis breweri</i>	5.0	(1.2)	0.56	6.3	(2.0)	0.39
<i>Danthonia intermedia</i>	1.8	(0.84)	0.29	1.3	(0.41)	0.39
<i>Deschampsia cespitosa</i>	1.0	(0.52)	0.13	0.17	(0.10)	0.087
<i>Elymus trachycaulus</i>	0.17	(0.17)	0.021	0.67	(0.56)	0.043
<i>Festuca rubra</i>				0.087	(0.087)	0.022
<i>Muhlenbergia filiformis</i>	1.25	(0.58)	0.19	1.5	(0.93)	0.13
<i>Muhlenbergia richardsonis</i>	0.042	(0.029)	0.042	0.54	(0.54)	0.022
<i>Muhlenbergia</i> sp.	0.063	(0.046)	0.042			
<i>Phleum alpinum</i>	0.15	(0.073)	0.083	0.065	(0.037)	0.065
<i>Poa pratensis</i>	0.21	(0.21)	0.021			
<i>Poa</i> sp.				0.065	(0.048)	0.043
<i>Ptilagrostis kingii</i>	12	(2.9)	0.38	17	(3.3)	0.54
<i>Trisetum spicatum</i>	0.23	(0.10)	0.13	0.022	(0.022)	0.022
unknown Poaceae	0.083	(0.066)	0.042	0.087	(0.068)	0.022

Table 14. Summary of results of all possible multiple regression models of terrestrial faunal order and total abundances on percent cover of individual plant taxa in Tuolumne. A “+” indicates that a given predictor was entered into a final model at $p < 0.025$; there were no significant negative coefficients. Models could not be constructed for leafhoppers, beetles, and ants/wasps.

	Response Variables					
	True bugs	Moths	Flies	Spiders	Mites	Total
R²	0.37	0.17	0.26	0.84	0.31	0.47
Predictors						
<i>Antennaria</i> sp.		+		+	+	+
<i>Carex utriculata</i>	+		+	+		+

Entered variables without significant effects on models:

Oreostemma spp.
Carex filifolia
Carex spp.
Calamagrostis breweri
Ptilagrostis kingii

Table 15. Summary of results of all possible multiple regressions models of Giant Forest terrestrial faunal order and total abundances on physical and coarse vegetation predictor variables. Positive or negative relationships indicate whether a given predictor was entered into a final model at “p” < 0.025 with a positive or negative coefficient (“+” or “-,” respectively). Predictors could not be successfully entered into models for moths.

	Response Variables							
	True bugs	Leafhoppers	Beetles	Wasps/Ants	Flies	Spiders	Mites	Total
R²	0.20	0.13	0.34	0.35	0.18	0.35	0.13	0.18
Predictors								
Soil Moisture	-					+		
Canopy Height			+	+	+	+		+
% Green Cover	+							
Patch Size			-				-	
<i>Entered variables without significant effects on models:</i>								
Percent Brown Cover								
Percent Litter								
Total Percent Cover								
Green Standing Crop								
Litter Mass								
Litter Depth								
Air Temperature								
Ground Temperature								
Relative Humidity								
Wind Speed								
Water Table Depth								
Soil Penetration Pressure								

Table 16. Mean percent (SE) cover of vegetation and frequency of occurrence in Giant Forest terrestrial plots (n= 48). Blanks, rather than “zeros,” are used to indicate that a given taxon was not collected. Continued next page.

	Mean	(SE)	Frequency
Equisetaceae			
<i>Equisetum arvense</i>	0.083	(0.065)	0.042
<i>Equisetum</i> sp.	0.021	(0.021)	0.021
Dennstaedtiaceae			
<i>Pteridium aquilinum</i>	0.17	(0.17)	0.021
Apiaceae			
<i>Oxypolis occidentalis</i>	2.1	(0.66)	0.35
Asteraceae			
<i>Madia bolanderi</i>	0.083	(0.083)	0.021
<i>Oreostemma</i> or <i>Erigeron</i> sp.	0.10	(0.10)	0.021
<i>Senecio clarkianus</i>	0.52	(0.33)	0.10
<i>Solidago californica</i>	0.042	(0.042)	0.021
<i>Solidago canadensis</i>	8.2	(2.6)	0.35
Caryophyllaceae			
<i>Stellaria</i> sp.	0.021	(0.021)	0.021
Ericaceae			
<i>Vaccinium uliginosum</i>	1.0	(1.0)	0.021
Fabaceae			
<i>Lotus oblongifolius</i>	0.63	(0.35)	0.15
Gentianaceae			
Unknown	0.042	(0.042)	0.021
Hypericaceae			
<i>Hypericum anagalloides</i>	1.8	(1.2)	0.083
Lamiaceae			
<i>Stachys albens</i>	1.3	(0.84)	0.23

Table 16 (cont.). Mean percent (SE) cover of vegetation and frequency of occurrence in Giant Forest terrestrial plots. Continued next page.

	Mean	(SE)	Frequency
<i>Stachys</i> sp.	0.042	(0.042)	0.021
Unknown	0.042	(0.029)	0.042
Malvaceae			
<i>Sidalcea oregana?</i>	0.021	(0.021)	0.021
<i>Sidalcea</i> sp.	0.063	(0.046)	0.042
Unknown	0.021	(0.021)	0.021
Onagraceae			
<i>Epilobium canum</i>	0.042	(0.042)	0.021
<i>Epilobium glaberrimum</i>	0.10	(0.10)	0.021
<i>Epilobium</i> sp.	0.042	(0.029)	0.042
Polygonaceae			
<i>Polygonum bistortoides</i>	0.88	(0.31)	0.27
<i>Polygonum</i> sp.	0.083	(0.083)	0.021
Primulaceae			
<i>Dodecatheon</i> sp.	0.81	(0.57)	0.062
Rosaceae			
<i>Potentilla</i> sp.	0.021	(0.021)	0.021
Rubiaceae			
<i>Galium triflorum</i>	0.021	(0.021)	0.021
<i>Galium</i> sp.	0.29	(0.21)	0.10
Saxifragaceae			
<i>Saxifraga oregana</i>	0.83	(0.59)	0.062
Scrophulariaceae			
<i>Castilleja</i> sp.	0.021	(0.021)	0.021
<i>Mimulus</i> sp.	0.10	(0.10)	0.021

Table 16 (cont.). Mean percent (SE) cover of vegetation and frequency of occurrence in Giant Forest terrestrial plots. Continued next page.

	Mean	(SE)	Frequency
Violaceae			
<i>Viola</i> sp.	0.46	(0.32)	0.10
Cyperaceae			
<i>Carex jonesii</i>	0.31	(0.31)	0.021
<i>Carex luzulina</i>	0.042	(0.042)	0.021
<i>Carex utriculata</i>	0.54	(0.52)	0.042
<i>Carex</i> sp.	9.5	(2.9)	0.56
<i>Eleocharis montevidensis</i>	0.73	(0.73)	0.021
<i>Eleocharis</i> sp.	5.0	(2.1)	0.23
<i>Scirpus congdonii</i>	0.13	(0.11)	0.042
<i>Scirpus microcarpus</i>	3.6	(1.3)	0.25
<i>Scirpus</i> sp.	1.5	(0.96)	0.19
Iridaceae			
<i>Sisyrinchium</i> sp.	0.042	(0.042)	0.021
Juncaceae			
<i>Juncus macrandrus</i>	0.063	(0.046)	0.042
<i>Luzula comosa</i>	0.042	(0.042)	0.021
Liliaceae			
<i>Camassia quamash</i>	0.042	(0.029)	0.042
<i>Lilium</i> sp.	0.10	(0.074)	0.042
<i>Tofieldia occidentalis</i>	0.021	(0.021)	0.021
<i>Veratrum californicum</i>	2.2	(1.1)	0.13
Unknown	0.021	(0.021)	0.021
Orchidaceae			
Unknown	0.042	(0.029)	0.042
Unidentified forb	0.25	(0.13)	0.13
Poaceae			
<i>Agrostis gigantea</i>	2.7	(2.0)	0.042

Table 16 (cont.). Mean percent (SE) cover of vegetation and frequency of occurrence in Giant Forest terrestrial plots.

	Mean	(SE)	Frequency
<i>Agrostis</i> sp. 1	0.56	(0.40)	0.042
<i>Agrostis</i> sp. 2	0.25	(0.25)	0.021
<i>Calamagrostis canadensis</i>	4.4	(2.6)	0.15
<i>Deschampsia cespitosa</i>	0.021	(0.021)	0.021
<i>Elymus glaucus</i>	5.2	(2.8)	0.13
<i>Elymus</i> sp.	0.10	(0.10)	0.021
<i>Glyceria elata</i>	0.46	(0.32)	0.042
<i>Glyceria</i> sp.	0.042	(0.042)	0.021
<i>Phleum pratense</i>	0.29	(0.25)	0.062
<i>Poa palustris</i>	0.42	(0.33)	0.042
<i>Poa pratensis</i>	4.8	(2.1)	0.19
<i>Poa</i> sp.	1.9	(0.76)	0.17
Unidentified monocot	0.021	(0.021)	0.021
Unidentified seedling	0.10	(0.10)	0.021

Table 17. Summary of results of all possible multiple regressions models of terrestrial faunal order and total abundances on percent cover of individual plant taxa in the Giant Forest. A “+” indicates that a given predictor was entered into a final model at $p < 0.025$; there were no significant negative coefficients. Predictors could not be successfully entered into models for moths or mites.

Response Variables							
	True bugs	Leafhoppers	Beetles	Wasps/Ants	Flies	Spiders	Total
R²	0.13	0.26	0.29	0.41	0.35	0.31	0.37
Predictors							
<i>Solidago canadensis</i>		+					
<i>Carex</i> spp						+	
<i>Scirpus microcarpus</i>				+	+	+	+
<i>Veratrum californicum</i>			+	+			
Poaceae	+	+	+	+	+	+	+
Entered variables without significant effects on models:							
<i>Eleocharis</i> sp							
<i>Agrostis gigantea</i>							
<i>Calamagrostis canadensis</i>							
<i>Elymus glaucus</i>							

Table 18. Trophic and ecological status of common taxa. Underlining indicates taxa collected primarily in aquatic samples. Continued next page.

Order Suborder	Family	Trophic/ecological status
Collembola	Entomobryidae Isotomidae	feed on decaying vegetation, fungi feed on decaying vegetation, fungi
Ephemeroptera	<u>Baetidae</u> <u>Ephemerellidae</u> <u>Heptogeniidae</u> <u>Leptophlebiidae</u> <u>Siphonuridae</u>	1° consumer, collector-gatherer, scraper 1° consumer, collector-gatherer 1°, 2° consumer, scraper, engulfer 1° consumer, collector-gatherer, scraper 1°, 2° consumer, collector-gatherer
Odonata Anisoptera Zygoptera	<u>Lestidae</u> <u>Libellulidae</u>	2°, 3° consumer, predator-engulfer 2°, 3° consumer, predator-engulfer
Plecoptera	<u>Nemouridae</u> <u>Leuctridae</u> <u>Chloroperlidae</u>	1° consumer, shredder, detritus 1° consumer, shredder, detritus 1°, 2° consumer, scraper, engulfer
Orthoptera	Acrididae	1° consumer
Hemiptera Heteroptera	<u>Notonectidae</u> Saldidae Miridae <u>Corixidae</u> Nabidae Anthracoridae Pentatomidae Lygaeidae	2° consumer, piercers, cannibals 2° consumer, insects 1°, 2° consumer, plants, insects 1°, 2° consumer, piercers, scrapers 2° consumer, larval & adult insects 2° consumer, eggs, larvae, small insects 1°, 2° consumers, insect eggs 1° consumer (seeds), some sap

Table 18 (cont.). Trophic and ecological status of common taxa. Continued next page.

Homoptera

Auchenorrhyncha	Cicadellidae	1° consumer, suck plant juices
	Delphacidae	1° consumer, suck plant juices
Sternorrhyncha	Psyllidae	1° consumer, honeydew for ants
	Aphididae	1° consumer, suck plant juices

Coleoptera

Adephaga	Carabidae	2° consumer as adult and larva
	<u>Dytiscidae</u>	1°, 2°, 3° consumers
Polyphaga	<u>Hydrophilidae</u>	2° consumer, larva, 1°, 2° consumer, adult
	<u>Hydraenidae</u>	1°, 2° consumers
	Ptiliidae	1° consumer, fungus, detritus
	Staphylinidae	2°, 3° consumers, some parasitic
	Scarabaeidae	feed on roots, feces, carrion
	<u>Scirtidae</u>	1° consumer, scraper, collector-gatherer
	Buprestidae	larval borers, adult 1° consumer
	Throscidae	1° consumer, in litter, on plants
	Elateridae	roots, 2° consumers, under bark
	Cantharidae	1°, 2° consumers, nectar, pollen, insects
	Trogossitidae	2° consumers, some 1°
	Cleridae	2° consumers
	Sphindidae	fungus
	Phalacridae	1° consumer, pollen, also fungus
	Coccinellidae	2° consumer, scale insects, eggs
	Latriidae	1° consumer, fungus
	Mordellidae	1° consumer, stems, dead wood, fungus
	Anthicidae	1° consumer, decaying, live veg
	Cerambycidae	1° consumer, wood, roots, leaves, pollen
	<u>Chrysomelidae</u>	1° consumer, stems, roots, leaves, pollen
	Curculionidae	1° consumer, roots, leaves, stems

Hymenoptera

Tenthredinidae	1° consumer, leaves, stems
Ceraphronidae	2°, 3° consumers/parasites
Braconidae	2° consumer, internal parasite
Ichneumonidae	2°, 3°, 4°, 5° consumers/parasites
Mymaridae	egg parasites
Pteromalidae	2°, 3°, 4° consumers/parasites
Figitidae	2°, 3° consumers/parasites
Proctotrupidae	2°, 3° consumers/parasites

Table 18 (cont.). Trophic and ecological status of common taxa. Continued next page.

Hymenoptera, cont.

Diapriidae	2°, 3° consumers/parasites
Scelionidae	egg parasites
Platygastridae	2°, 3° consumers/parasites
Sphecidae	2°, 3°, 4° consumers/parasites
Colletidae	pollen, nest in cavities and stems
Pompilidae	2°, 3° consumers/parasites, spiders
Formicidae	1°, 2°, 3° consumers, honeydew

Trichoptera

<u>Polycentropodidae</u>	1°, 2° consumers, collectors, engulfers
<u>Limnephilidae</u>	1° consumer, detritus, collector-gatherer
<u>Brachycentridae</u>	1° consumer, collectors, shredders

Lepidoptera

Acanthopteroctetidae	1° consumer, leaf miners, pollen
Gracillariidae	1° consumer, leaf miners
Elachistidae	1° consumer, leaf miners
Coleophoridae	1° consumer, case-builder
Gelechiidae	1° consumer, bores stems, leaves
Pyrilidae	1°, 2° consumers, borers
Crambidae	1° consumer, bores stems, roots
Noctuidae	1° consumer, foliage, some borers

Diptera

Nematocera	<u>Tipulidae</u>	1°, 2° consumers, shredders, engulfers
	Psychodidae	1° consumer (larva), 2° consumer(adult)
	<u>Ceratopogonidae</u>	2°, 3°, 4° consumers, nectar
	<u>Chironomidae</u>	detritus, opportunists
	<u>Culicidae</u>	2°, 3°, 4° consumers, nectar, sap
	<u>Dixidae</u>	1° consumer, detritus, collector-gatherer
	<u>Simuliidae</u>	1° consumer, detritus, collector-filterer
	<u>Bibionidae</u>	feces, decaying wood, roots
	Cecidomyiidae	1°, 2° consumers, decaying wood
	Mycetophylidae	fungus, 2° consumers
	Scatopsidae	decaying matter, feces, bark
	Sciaridae	fungus, forms crawling masses

Table 18 (cont.). Trophic and ecological status of common taxa. Continued next page.

Diptera, cont.

Brachycera	Athericidae	2° consumers (larva), honeydew (adult)
	<u>Tabanidae</u>	2° consumers, piercers
	Empididae	1°, 2° consumers, insects, nectar, pollen
	Dolichopodidae	2° consumers, damp meadows
	Lonchopteridae	1° consumer, nectar
	Pipunculidae	3° consumers, Homopteran parasites
	Phoridae	2°, 3°, 4° consumers, parasites
	Anthomyiidae	2° consumers, parasites
	Hippoboscidae	3°, 4° consumers, suck bird blood
	Muscidae	1°, 2° consumers, feces, carrion
	Tachinidae	2°, 3° consumers, parasites
	Tephritidae	1° consumer, fruit, seeds, leaves
	Sepsidae	feces, carrion, decaying vegetation
	Clusiidae	decaying wood, larvae can “leap”
	Chloropidae	1°, 2°, 3° consumers, spider eggs
	Heleomyzidae	decaying plant and animal matter
	Sphaeroceridae	feces, decaying matter, fungi
	Diastatidae	unknown
	Drosophilidae	1° consumer, decaying litter, fruit, fungus
	Ephydriidae	1°, 2° consumers, mostly microphagous

Araneae

Araneidae	2°, 3° consumers, orb weavers
Tetragnathidae	2°, 3° consumers, orb weavers
Linyphiidae	2°, 3° consumers, sheet/dome web
Dictynidae	2°, 3° consumers, build snares in foliage
Agelenidae	2°, 3° consumers, funnel webs
Oxyopidae	2°, 3° consumers, forage in foliage
Pisauridae	2°, 3° consumers, often aquatic insects
Lycosidae	2°, 3° consumers, foraging or web
Clubionidae	2°, 3° consumers, forage at night
Anyphaenidae	2°, 3° consumers, forage in foliage
Gnaphosidae	2°, 3° consumers, forage at night
Philodromidae	2°, 3° consumers, forage on leaves. stems
Thomisidae	2°, 3° consumers, ambush prey
Salticidae	2°, 3° consumers, stalk prey